New Morphological Evidence for the Phylogeny of Artiodactyla, Cetacea, and Mesonychidae

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ABSTRACT

Parsimony-based analyses of a data set including 68 taxa coded for 186 morphological characters corroborate monophyly of Artiodactyla (even-toed ungulates), Suiformes (hippos, pigs, peccaries), Neoselenodontia (camels, deer, cows), and Acreodi (whales, dolphins, porpoises, mesonychids). Additional findings include a sister-group relationship between Cainotheriidae and Cameloidea (Camelidae + Oromerycidae), *Elomeryx* as the sister group to all other suiform artiodactyls, Protoceratidae as the basal branch of Neoselenodontia, and paraphyly of Mesonychidae. The molecule-based groups Whippomorpha (whales, dolphins, hippos), Cetruminantia (whales, deer, cows), and Artiofabula (whales, cows, pigs) are contradicted by these data and occur together in trees that are at least 25 steps longer than the most parsimonious ones. In terms of tree length, the molecule-based topology is contradicted by morphological data with and without extinct taxa, and unlike previous, morphology-based analyses, the exclusion of Cetacea from the clade of living artiodactyls is not dependent on the inclusion of extinct taxa. Artiodactyla is diagnosed in all most parsimonious trees by several characters, including a short mastoid process of the petrosal, absence of an alisphenoid canal, and presence of an entocingulum on P4. Some previously suggested artiodactyl synapomorphies, such as an enlarged facial exposure of the lacrimal and absence of contact between the frontal and alisphenoid, are shown to be synapomorphies of more exclusive clades within Artiodactyla.

INTRODUCTION

The phylogenetic position of Cetacea (whales, dolphins, and porpoises) is one of the most hotly debated issues in mammalian systematics, as shown by a review of the controversy surrounding cetacean and artiodactyl phylogeny (Luo, 2000), a volume on

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cetacean origins (Thewissen, 1998), and numerous analytical studies (e.g., Gatesy et al., 1999a, 1999b; Nikaido et al., 1999; O'Leary, 1999; O'Leary and Geisler, 1999; Shimamura et al., 1999). Almost all morphology-based studies have found Mesonychidae (or one or more mesonychids) to be the sister group to Cetacea, and have found Artiodactyla (even-hoofed ungulates, including camels, pigs, and deer) to be monophyletic (Van Valen, 1966; Thewissen, 1994; Geisler and Luo, 1998; O'Leary, 1998a; O'Leary and Geisler, 1999; Luo and Gingerich, 1999) (fig. 1A). By contrast, the vast majority of DNA sequence-based studies have found strong evidence for two clades that render Artiodactyla paraphyletic: (1) Whippomorpha, which includes Hippopotamidae and Cetacea, and (2) Cetruminantia, which includes Whippomorpha and Ruminantia (includes deer, cows, antelope, chevrotain, and many others) (Gatesy et al., 1996, 1999a, 1999b; Gatesy, 1997, 1998; Montgelard et al., 1997; Shimamura et al., 1997, 1999; Ursing and Arnason, 1998; Nikaido et al., 1999; Kleineidam et al., 1999) (fig. 1B). The incongruence between morphological and molecular data is statistically significant (O'Leary, 1999), and there are no plausible explanations for the conflict between the two classes of data.

Incongruence between different classes of data can be objectively measured only if the character data have been compiled in the form of a character/taxon matrix. The specific observations that lead to the incongruence can be isolated and reexamined if the data are in a matrix form. Although there have been numerous studies on artiodactyl phylogeny (e.g., Matthew, 1929, 1934; Janis and Scott, 1987; Gentry and Hooker, 1988; Scott and Janis, 1993) and others on cetacean phylogeny (e.g., Muizon, 1991; Fordyce, 1994; Messenger and McGuire, 1998; Luo and Gingerich, 1999; Uhen, 1999), there have been few studies that have made comparisons between members of both taxonomic groups. Geisler and Luo (1998) presented the first cladistic analysis of morphological data that included basal cetaceans as well as several artiodactyls. Their work was significantly expanded and improved upon by Geisler and O'Leary (1997) and O'Leary and

Geisler (1999). Although these studies have made detailed comparisons between morphological and molecular data possible, much of the data concerning the phylogeny within Artiodactyla have yet to be included. This study has four primary goals: (1) to add taxa and new characters to previously published morphological data sets (Geisler and Luo, 1998; O'Leary and Geisler, 1999; Luo and Gingerich, 1999); (2) to determine what taxonomic groups these characters support, as well as the degree of support for these groups; (3) to determine if the evidence for the exclusion of Cetacea from the clade of extant artiodactyls is restricted to the data for extinct taxa; and (4) to test alternative phylogenies, particularly those based on molecules.

Taxonomy

The molecule-based and morphology-based hypotheses of artiodactyl and cetacean phylogeny not only differ in the phylogenetic position of extant cetaceans and extant artiodactyls, but they are based on significantly different, yet slightly overlapping, sets of taxa. The disparity in topology and in the choice of taxa highlights the confusion caused by phylogenetic definitions for taxa. Some of the taxa discussed in this paper have not been properly or explicitly defined, while the use of other taxa varies between authors. For instance, Artiodactyla has either not included Cetacea (Simpson, 1945; McKenna and Bell, 1997), has included Cetacea (Graur and Higgins, 1994; Xu et al., 1996; Kleineidam et al., 1999), or has been replaced by the taxon Cetartiodactyla, which includes Cetacea (Montgelard et al., 1997; Nikaido et al., 1999). The inclusion of Cetacea within Artiodactyla, as advocated by Graur and Higgins (1994), Xu et al. (1996), and Kleineidam et al. (1999), can be justified if their molecule-based cladograms are the most parsimonious hypotheses and if they use a phylogenetic definition for Artiodactyla.

Taxa that have been defined using phylogenetic taxonomy (sensu stricto de Quieroz and Gauthier, 1990) are not used in this paper because taxon membership varies significantly with the choice of cladogram. To avoid confusion, only group-based definitions are used here. The content of each

group follows McKenna and Bell (1997), with the following exceptions. Suiformes is redefined here as the group including Anthracotheriidae, Entelodontidae, Hippopotamidae, Suidae, and Tayassuidae but excluding Ruminantia, Camelidae, Oromerycidae, Cainotheriidae, Oreodontoidea, Xiphodontidae, *Mixtotherium, Cebochoerus, Gobiohyus, Homacodon,* and all species of *Diacodexis.* Simpson (1945) and McKenna and Bell (1997) placed all nonselenodont artiodactyls in Suiformes, which makes the group paraphyletic with respect to virtually all morphology-based hypotheses of artiodactyl phylogeny (Matthew, 1934; Gentry and Hooker, 1988; Geisler and Luo, 1998; O'Leary and Geisler, 1999). The present redefinition maintains traditional members of this group, such as Suidae and Hippopotamidae, but excludes former members so that it becomes monophyletic, at least based on morphological data. If future parsimony-based phylogenies have a paraphyletic Suiformes, I suggest that this group be abandoned instead of being redefined.

As in Simpson (1945), but unlike McKenna and Bell (1997), Suina is used to denote the group including Suidae and Tayassuidae to the exclusion of Hippopotamidae and other suiform artiodactyls. McKenna and Bell (1997) did not recognize this clade in their classification and instead listed Suina as a junior synonym of Suinae. Following Viret (1961) and Webb and Taylor (1980), but contrary to McKenna and Bell (1997) and Gentry and Hooker (1988), Ruminantia, as used here, does not include the Amphimerycidae. Instead, Amphimerycidae and Xiphodontidae are considered as the only two families in the group Xiphodontoidea, named by Viret (1961). Use of the group Neoselenodontia follows Webb and Taylor (1980) and includes Camelidae, Oromerycidae, Ruminantia, Protoceratidae, and Xiphodontoidea but excludes Oreodontoidea. McKenna and Bell (1997) elevated Acreodi to subordinal rank and placed triisodontids, mesonychids, and hapalodectids inside it; however, I follow the use of Acreodi by Prothero et al. (1988) to denote the group including Hapalodectidae, Mesonychidae, and Cetacea. *Andrewsarchus* is excluded from Acreodi based on previous morphological studies (O'Leary, 1998a;

Geisler and Luo, 1998; O'Leary and Geisler, 1999). McKenna and Bell (1997) did not provide a name for the group that includes Cetacea, Artiodactyla, Mesonychidae, Hapalodectidae, and *Andrewsarchus.* Following Thewissen (1994) and Geisler and Luo (1998), I use Paraxonia for this group, which McKenna and Bell listed as a junior synonym of Artiodactyla.

PREVIOUS STUDIES

Molecular and morphological studies on the phylogenetic position of Cetacea have been reviewed by Gatesy (1998) and O'Leary and Geisler (1999); only recently published papers not reviewed by these authors will be described here. Gatesy (1998) presented new nucleotide sequences for several mammalian taxa and performed combined and partitioned analyses of his data set, which included over 4500 aligned nucleotide positions. His analysis with all genes combined and most of his partitioned analyses supported a sister-group relationship between Hippopotamidae and Cetacea, as well as a larger clade including these two taxa plus Ruminantia. These controversial clades that result in artiodactyl paraphyly received significant branch support and had bootstrap values over 90% (Gatesy, 1998). Luckett and Hong (1998) presented an exhaustive analysis of selected morphological characters and previously published or available cytochrome *b* sequences. They found that two characters, the double-trochleated astragalus and a trilobed, deciduous, fourth lower premolar, are rare among mammals but occur in every extant and extinct artiodactyl genus for which these anatomical regions are preserved. They also determined that most of the nucleotides that supported the Hippopotamidae + Cetacea clade exhibit some level of homoplasy across all mammals. Based on these observations, Luckett and Hong (1998) concluded that existing molecular data are not sufficient to overturn artiodactyl monophyly; however, other genes that corroborate Whippomorpha and Cetruminantia (e.g., κ and β casein and γ fibrinogen) were not discussed in much detail.

Ursing and Arnason (1998) sequenced the entire mitochondrial genome of *Hippopota-*

mus amphibius and included it in a phylogenetic analysis with 15 other mammals. Maximum likelihood, maximum parsimony, and neighbor-joining methods produced optimal trees that supported a hippopotamid and cetacean clade as well as a hippopotamid, cetacean, and ruminant clade. Milinkovitch et al. (1998) retrieved nucleotide sequences of the α-lactalbumin protein from several artiodactyls and cetaceans. Using a variety of phylogenetic methods, they found additional support for artiodactyl paraphyly; however, their taxonomic sampling was poor (only four cetaceans and four artiodactyls). Montgelard et al. (1998) completed the first phylogenetic analysis of higher level artiodactyl phylogeny that combined morphological and molecular data; however, little new data were presented, Cetacea was not included, and the ingroup only included six taxa. They found substantial support for Suina (Suidae + Tayassuidae) but weak support for a suiform clade of Suina + Hippopotamidae.

Gatesy et al. (1999b) added several previously published data sets to that of Gatesy (1998), resulting in a 64% increase in the number of informative characters. They also defined and implemented several new methods of evaluating nodal support, resulting in the discovery of significant amounts of hidden support for the Hippopotamidae + Cetacea clade as well as the more inclusive clade including Cetacea, Hippopotamidae, and Ruminantia (Gatesy et al., 1999b). Four new sequences were added to a growing body of molecular data by Gatesy et al. (1999a). These new sequences plus previously published data were compiled into a data set (WHIPPO-1), which resulted in a 67% increase in the number of informative characters over Gatesy et al. (1999b). The most parsimonious trees for the WHIPPO-1 matrix were the same as those for the matrix analyzed by Gatesy et al. (1999b) but had increased support for the controversial clades that group cetaceans with extant artiodactyls. The cost of artiodactyl monophyly was approximately 120 steps (Gatesy et al., 1999a). Gatesy et al. (1999a) also presented and analyzed a larger matrix dubbed WHIPPO-2. Like many previous molecule-based hypotheses, all most parsimonious trees had a

monophyletic Whippomorpha, Cetruminantia, and Artiofabula (fig. 1B).

O'Leary (1999) presented the first combined morphological and molecular analysis that included significant numbers of cetaceans and artiodactyls. The morphological data were based on the matrix of O'Leary and Geisler (1999), and the molecular data came primarily from Gatesy et al. (1996) and Gatesy (1997). O'Leary (1999) found the incongruence between the neontological (almost entirely molecular) and osteological partitions to be statistically significant according to the partition-homogeneity test of Farris et al. (1995). Sequence alignments and analyses of the combined matrix were performed using nine different combinations of parameters (e.g., gap cost, transition/transversion ratio), and all resulted in a paraphyletic Artiodactyla. Apparently all most parsimonious trees from all analyses had the Hippopotamidae and Cetacea clade to the exclusion of other extant artiodactyls (O'Leary, 1999).

Shimamura et al. (1999) expanded upon the work of Shimamura et al. (1997) by sequencing and comparing more nucleotide sequences for several different SINEs (short interspersed repetitive elements) found in some artiodactyls and cetaceans. The identification of related SINEs in *Sus* (pigs) and *Tayassu* (peccaries) but not in *Camelus* (camels) corroborated the phylogeny of Gatesy (1998: fig. 16), where Suidae and Tayassuidae are more closely related to cetaceans than is Camelidae. Nikaido et al. (1999) presented new SINE and LINE (long interspersed element) data, including the distribution of SINEs at 10 new loci. In addition to corroborating the phylogeny of Shimamura et al. (1997, 1999), they found four insertions that support the Hippopotamidae and Cetacea clade. Nikaido et al. (1999) asserted that SINEs are virtually homoplasy-free and that their insertions can be treated as irreversible; however, considering the small number of SINE characters and the large amount of missing data in the matrix of Nikaido et al. (1999), such claims are premature. As with all other phylogenetic data, their only source of validation is congruence with preexisting, independent data, in this case nucleotide distributions.

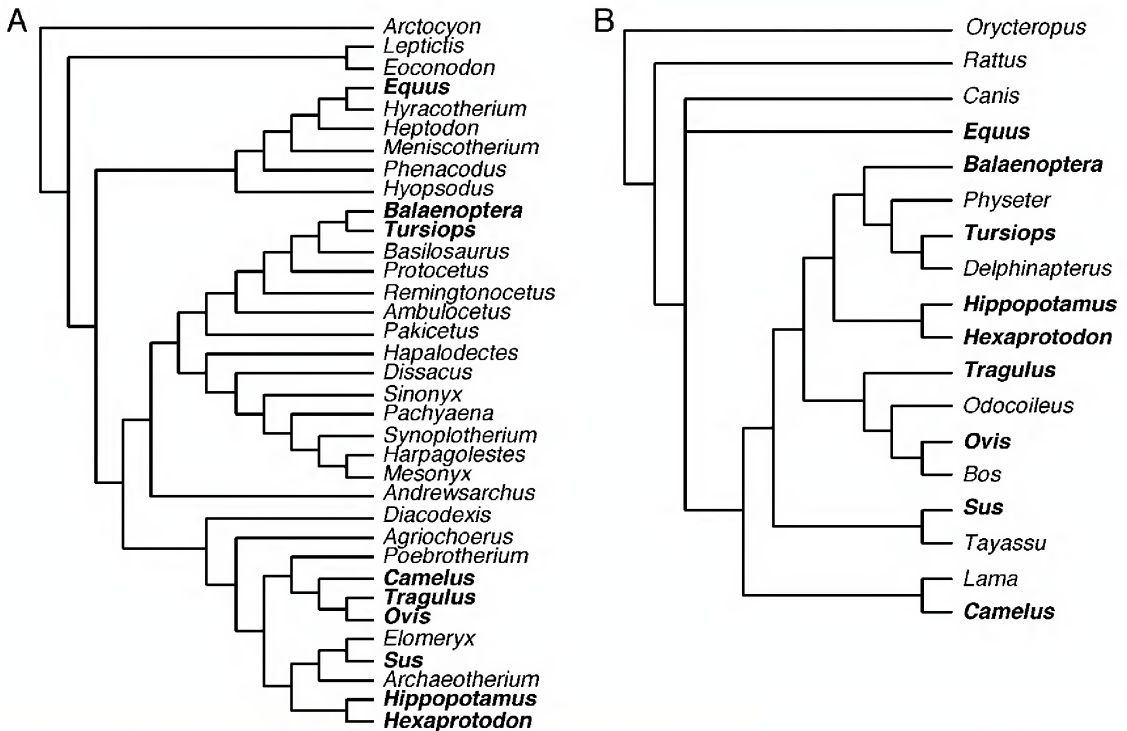Kleineidam et al. (1999) sequenced pan-

Fig. 1. Previous phylogenetic hypotheses for artiodactyls, cetaceans, and mesonychids. Taxa not included in this study were pruned from each tree, and taxa shared between the previous two studies are in boldface. **A.** The most parsimonious tree for the morphological data analyzed by O'Leary and Geisler (1999). Note that Artiodactyla, Neoselenodontia, and Suiformes are monophyletic. **B.** The strict consensus of the shortest trees for the WHIPPO-2 molecular data set of Gatesy et al. (1999a). Unlike O'Leary and Geisler (1999), Artiodactyla, Neoselenodontia, and Suiformes are paraphyletic, while Whippomorpha, Cetruminantia, and Artiofabula are monophyletic.

creatic ribonuclease genes for eight artiodactyls and cetaceans. A phylogenetic analysis of these sequences plus previously published data supported a *Hippopotamus* and Cetacea clade; however, unlike other recent molecular studies, Suidae (pigs) instead of Camelidae was the sister group to a clade including all other extant artiodactyls and Cetacea. Waddell et al. (1999), in a summary paper for the 1998 "International Symposium on the Origin of Mammalian Orders", presented no new data or analyses but did name several controversial clades of artiodactyls supported by molecular data. The clade of Cetacea + Hippopotamidae was named Whippomorpha, the Whippomorpha + Ruminantia clade was named Cetruminantia, and the Whippomorpha + Suidae (and presumably Tayassuidae) was named Artiofabula (Waddell et al., 1999).

O'Leary and Geisler (1999) presented a detailed phylogenetic analysis of a matrix of 40 taxa scored for 123 morphological characters, a significant increase in both characters and taxa over the data set used by Geisler and Luo (1998). Their most parsimonious trees included a monophyletic Artiodactyla, Mesonychidae + Cetacea, Neoselenodontia, and Suiformes (O'Leary and Geisler, 1999) (fig. 1A). They found that the recovery of artiodactyl monophyly hinged on the addition of extinct taxa to the phylogenetic analysis. Thewissen and Madar (1999) described the functional morphology of the ankle in ungulates, listed eight phylogenetically informative characters of this region (some new and others previously described), and presented a character matrix of ankle characters scored for a diverse group of mammals. Most of the new data in the matrix was

based on several astragali that were referred to cetaceans by Thewissen et al. (1998); however, O'Leary and Geisler (1999) questioned their referral because it is based on size and faunal components, not on direct association with definitive cetacean remains. The matrix of Thewissen and Madar (1999) was analyzed by calculating the fit of all characters to the tree of Prothero et al. (1988) or to modified versions of this tree. They state that tarsal morphologies are "also consistent with the inclusion of cetaceans in artiodactyls, if one assumes that the wide arc of rotation of the trochleated head was lost during the origin of Cetacea" (Thewissen and Madar, 1999: 28). However, the only cladogram in their figure 2 that had Cetacea grouped within Artiodactyla was five steps longer than alternative topologies that placed Cetacea outside of, but still the sister group to, Artiodactyla.

Luo and Gingerich (1999) described the basicrania of several basal cetaceans and mesonychids, determined the homologs of highly derived cetacean basicranial structures in other terrestrial mammals, and presented a parsimony-based analysis of 64 basicranial characters. Their phylogenetic analysis supported a sister group relationship between Cetacea and Mesonychidae, and they listed several characters that support this clade; however, artiodactyl monophyly was not tested because only one artiodactyl taxon, *Diacodexis,* was included. O'Leary and Uhen (1999) added the taxon *Nalacetus* to the matrix of O'Leary and Geisler (1999) and tested hypotheses concerning the stratigraphic fit of the most parsimonious trees and the relative timing of the evolution of characters. Their most parsimonious trees are identical to those of O'Leary and Geisler (1999) except that *Harpagolestes* was the sister group to *Synoplotherium* instead of *Mesonyx.*

INSTITUTIONAL ABBREVIATIONS

AMNH-M	Department of Mammalogy, Division of Vertebrate Zoology, American Museum of Natural History, New York
AMNH-VP	Division of Paleontology (vertebrate collection only), American Museum of Natural History, New York
ChM PV	Charleston Museum vertebrate paleontology collection, Charleston, South Carolina
GSM	Georgia Southern Museum, Statesboro, Georgia.
GSP-UM	Geological Survey of Pakistan/University of Michigan, Ann Arbor
H-GSP	Howard University/ Geological Survey of Pakistan, Washington, D.C.
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
MAE	Mongolian Academy of Sciences–American Museum of Natural History Paleontological Expeditions, collection to be deposited at the Mongolian Academy of Sciences, Ulaan Bataar
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
YPM	Yale Peabody Museum, New Haven, Connecticut
YPM-PU	Princeton University collection (now at Yale Peabody Museum)

MATERIALS AND METHODS

TAXON SAMPLING

In general, taxa were chosen to adequately sample the diversity of Artiodactyla, Mesonychidae, and Cetacea (O'Leary and Geisler, 1999; method 3 of Hillis, 1998). Most OTUs (operational taxonomic units) were genera, leaving monophyly of more inclusive taxa to be tested. Extant genera, which were used as taxonomic exemplars in the molecular studies of Gatesy (1998) and Gatesy et al. (1999a), were also included to facilitate a combined molecule and morphology phylogenetic analysis (Geisler, work in progress). The selection of extinct taxa was based on simulation studies, which show that phylogenetic accuracy can be increased by breaking up long branches, where branch length is the number of evolutionary events (Graybeal, 1998; method 4 of Hillis, 1998). The phylogeny of Artiodactyla and Cetacea likely contains long branches because many of the branching events occurred in the Late Cretaceous or Paleocene (O'Leary and Geisler, 1999). At least 89% of Artiodactyla, Cetacea,

and close relatives are extinct (O'Leary and Geisler, 1999); therefore, including extinct taxa for consideration greatly increases the pool of taxa that likely attach near the bases of long branches.

Several model-based studies have shown that long branch attraction is a potential problem for phylogeny reconstruction using parsimony, and that taxonomic sampling can be used to reduce this problem. Felsenstein (1978) demonstrated that, given a model of evolution that specifies probabilities of stasis or change between character states, phylogenies that have long terminal branches separated by short internal branches will be incorrectly reconstructed using parsimony. Hendy and Penny (1989) suggested that this problem could be alleviated by adding taxa that attach to the base of long branches. Their suggestion has been supported by the work of Hillis (1998) and Graybeal (1998).

Kim (1996) described apparently counterintuitive examples of phylogenies that led to incorrect reconstructions using parsimony regardless of the number and type of taxa sampled. His examples required that sampling be restricted to subtrees within the entire phylogeny, and he calculated the inconsistency using fixed probabilities for estimating the correct phylogeny of each subtree. Actual studies are not restricted to sampling within parts of the phylogeny, except possibly by extinction or the absence of fossils; therefore, the probabilities of correctly estimating subtrees depend on the sampling of taxa. Adding taxa that break up long branches can increase the probability of getting the wrong tree with parsimony if the branch lengths of the added taxa are longer than the original inconsistent branch (Kim, 1996). Both Kim (1996) and Hulsenbeck (1991) showed that the converse is also true, that the inconsistency can be removed if the added taxa have very short terminal branches. Extinct taxa that are found in strata near the age of speciation events of interest (i.e., disputed nodes) are expected to have shorter branch lengths because "they had less time to evolve" (Gauthier et al., 1988: 193). Many of the taxa used in this study are from the Paleocene and Eocene (McKenna and Bell, 1997) and are close in time to the estimated origin of the most exclusive clade for which they are members.

The ingroup for this study included 10 cetaceans, 9 mesonychids, 2 hapalodectids, 32 artiodactyls, 4 perissodactyls (horses, rhinos, tapirs), and 6 archaic ungulates (appendix 1). In comparison to O'Leary and Geisler (1999), which is the most comprehensive morphological analysis of artiodactyls and cetaceans to date, the present study includes 28 additional taxa. Leptictidae and *Orycteropus* were included as outgroups and were used to root all most parsimonious trees. The exclusion of Leptictidae from the ingroup was supported by Novacek (1986, 1992), and *Orycteropus* was outside of the clade including artiodactyls and cetaceans in the most parsimonious trees of morphological studies (Novacek, 1986, 1992; Gaudin et al., 1996; Shoshani and McKenna, 1998), molecule-based analyses (Stanhope et al., 1996; Gatesy et al., 1999b), and one combined analysis (Liu and Miyamoto, 1999). Two carnivores (*Canis* and *Vulpavus*) and *Rattus* were added to aid in a project that will integrate the current data set with previously published molecular data (Geisler, in prep.). *Diacodexis* is a critical but problematic early artiodactyl taxon. It was split into two OTUs: *Diacodexis pakistanensis* and North American Wasatchian *Diacodexis,* with the latter being based primarily on specimens referred to *D. metsiacus* (Rose, 1985). The allocation of species to *Elomeryx* follows MacDonald (1956), and the allocation of specimens to *Pakicetus* follows Thewissen and Hussain (1998). Most taxa were scored from specimens in the vertebrate paleontology and mammalogy collections at the American Museum of Natural History (appendix 1).

CHARACTER DATA

Each of the 68 ingroup and outgroup taxa were scored for the 186 morphological characters listed in appendix 2, with codings for each taxon listed in appendix 3. Of the 186 morphological characters, approximately 47 are original to this work, while the remaining characters are from previous morphological studies (Webb and Taylor, 1980; Novacek, 1986; Janis and Scott, 1987; Gentry and Hooker, 1988; Scott and Janis, 1993; Thewissen and Domning, 1992; Thewissen, 1994; Geisler and Luo, 1998; O'Leary, 1998a;

O'Leary and Geisler, 1999; Luo and Gingerich, 1999). An attempt was made to include all previously published morphological characters useful in determining whether or not Cetacea belongs within the clade of living artiodactyls. Considering the diversity of taxa that belong within the ingroup, as well as the volume of previous work on artiodactyl phylogeny, my goal was probably unrealistic; however, this matrix does provide a useful contribution for those wishing to pursue this problem further. In comparsion to O'Leary and Geisler (1999), the present study includes an additional 63 morphological characters. Subheadings within the character list in appendix 2 denote groups of characters that occur in the same anatomical region or share a common function.

SELECTED CHARACTER DESCRIPTIONS

Of the 186 morphological characters in this study, I have selected 11 of them that are either potential synapomorphies of Artiodactyla or synapomorphies of a more inclusive mammalian clade. In cases where descriptions are insufficient, I have included illustrations. For additional descriptions of basicranial characters, see Geisler and Luo (1998) and Luo and Gingerich (1999), and for descriptions of dental characters, see Gentry and Hooker (1988) and O'Leary (1998a).

Character 49: Alisphenoid canal (alar canal).—Present (0); absent (1) (Novacek, 1986; Thewissen and Domning, 1992). The alisphenoid canal transmits the infraorbital ramus of the maxillary artery (Wible, 1987; Evans, 1993), and if the foramen rotundum opens into the medial wall of the alisphenoid canal, then the anterior half of the canal also carries the maxillary branch of the trigeminal nerve (Sisson, 1921; Evans, 1993). For the group of taxa studied here, most of the primitive taxa have an alisphenoid canal, including Leptictidae, *Eoconodon, Hyopsodus, Phenacodus,* and *Meniscotherium* (state 0). These observations are consistent with the view of Thewissen and Domning (1992) that presence of the canal is primitive for Eutheria.

The alisphenoid canal is absent in all artiodactyls except for *Cainotherium* (Hürzeler,

1936: pl. 2, figs. 2, 3); therefore, it is a potential synapomorphy of Artiodactyla. In the ruminants *Bos* and *Ovis* and in the suid *Sus* the alisphenoid canal is absent and the infraorbital ramus of the maxillary artery is lateral to the alisphenoid (state 1) (Getty, 1975). The alisphenoid canal is also absent in all extant cetaceans, and as in most artiodactyls the infraorbital ramus of the maxillary artery is lateral to the alisphenoid (Fraser and Purves, 1960). Absence of the alisphenoid canal also occurs in the most basal cetaceans *Pakicetus* and *Ambulocetus*; however, its absence in cetaceans may not be synapomorphic with the morphology of most artiodactyls because the probable sister groups of Cetacea, the Mesonychidae and Hapalodectidae, have an alisphenoid canal (Geisler and Luo, 1998).

Character 96: P^4 entocingulum.—Present, partially or completely surrounds the base of the protocone (0); absent or very small (1). If present, the entocingulum of P^4 is on the lingual margin of the tooth. In the artiodactyl *Elomeryx,* P^4 has an entocingulum that begins at the parastyle, wraps around the base of the protocone, and ends at the metastyle (state 0). The cingulum is separated from adjacent parts of the tooth by a deep groove except for its lingualmost portion, which is appressed to the base of the protocone (fig. 2A: en). Although most basal artiodactyls have a well-defined entocingulum, it is absent in most extant artiodactyls including all ruminants except for *Hypertragulus,* camelids, *Sus,* and *Tayassu* (state 1). An entocingulum occurs on the P^4 of the early cetaceans *Pakicetus* and *Georgiacetus,* although it is absent in *Basilosaurus.* In contrast to basal cetaceans, there is no entocingulum on the P^4 of all mesonychids, such as *Harpagolestes* (fig. 2B) (state 1).

Character 124: Occipital condyles.—Broadly rounded in lateral view (0); V-shaped in lateral view, in posterior view the condyle is divided into a dorsal and a ventral half by a transverse ridge (1). The occipital condyles of many mammals, such as in *Orycteropus* and *Phenacodus,* are smoothly convex and do not have a transverse ridge (state 0). By contrast, in most artiodactyls the occipital condyle has a transverse ridge that divides it into dorsal and ventral halves (state 1). The ridge begins at the lateral edge of the
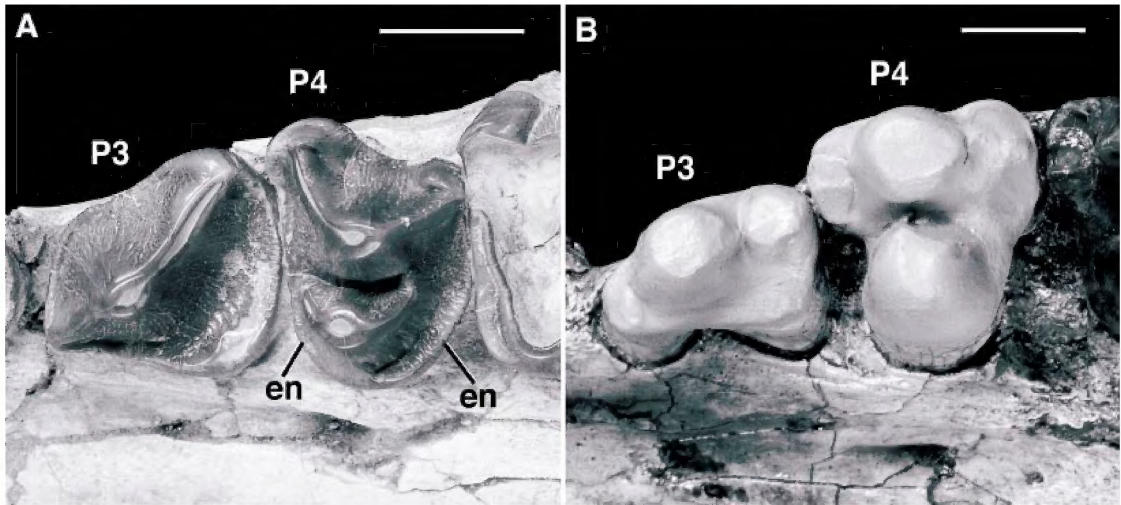
Fig. 2. Representative morphologies for the lingual margin of P^4. Labial is toward the top of the page, anterior is to the left, and the scale bars represent 10 mm. **A.** The third and fourth upper premolars of the artiodactyl *Elomeryx armatus* (AMNH 582). Note the presence of a prominent entocingulum that nearly encircles the base of the protocone. An entocingulum on P4 is widely distributed among basal artiodactyl taxa; therefore, it is a potential synapomorphy of Artiodactyla. **B.** The third and fourth upper premolars of the mesonychid *Harpagolestes orientalis* (AMNH 26300). Note the complete absence of an entocingulum on P^4. Abbreviations: en, entocingulum; P3, upper third premolar; P4, upper fourth premolar.

condyle and stretches across its entire posterior aspect. In lateral view the ridge gives the condyle a V-shaped profile. The vertex of the "V" is the top of the ridge, and in the artiodactyl *Poebrotherium* the vertex points ventrally and slightly posteriorly (fig. 3: or). The functional morphology of the ridge is unknown; however, I suspect it works with the alar and lateral atlanto-occipital ligaments to temporarily lock the occipital/atlas joint in the position that most efficiently orients the head for feeding. When the muscles that nod the head are relaxed, the morphology of the joint and the tension in the ligaments would passively restore the head to its former position.

Character 135: Entepicondylar foramen.—Present (0); absent (1) (Thewissen and Domning, 1992). The entepicondylar foramen transmits the median nerve and the brachial artery, as in the carnivore *Felis* (Crouch, 1969). It is located on the distal end of the humerus and perforates the proximal half of the medial epicondyle. Shoshani (1986) hypothesized that presence of an entepicondylar foramen was primitive for eutherian mammals. His view is supported here because an entepicondylar foramen occurs in most of the archaic taxa surveyed in this study, including Leptictidae, *Orycteropus, Vulpavus, Arctocyon, Eoconodon, Hyopsodus, Phenacodus,* and *Meniscotherium.* The entepicondylar foramen is absent in all artiodactyls, and thus its absence is a potential synapomorphy of that group. It is also absent in all cetaceans, perissodactyls, the carnivore *Canis,* and the rodent *Rattus* (state 1).

Character 152: Third trochanter of femur (ordered).—Present (0); highly reduced (1); absent (2) (Luckett and Hong, 1998; O'Leary and Geisler, 1999). The third trochanter is a flange that projects from the lateral side of the humeral shaft. On average, it is situated at one third of the distance from the proximal to the distal end of the humerus. The superficial gluteus muscle, which extends the hindlimb at the hip joint (Evans, 1993), inserts on the third trochanter. In ruminants, which lack a third trochanter, the superficial gluteus has fused with the biceps femoris to form a gluteobiceps. Instead of inserting on the femur, the gluteobiceps inserts on the crural facia, lateral patellar ligament, and facia lata (Getty, 1975). Presence of a large,

Fig. 3.   Oblique posterolateral view of the right occipital condyle of *Poebrotherium* (AMNH 42257), with right and left stereopair views. The occipital condyle is divided into dorsal and ventral halves by a transverse ridge. The occipital ridge is a potential synapomorphy of Artiodactyla. Scale bar is 10 mm in length. Abbreviations: fm, foramen magnum; or, occipital ridge; tb, tympanic bulla.

square-shaped third trochanter is probably primitive for the ingroup because it is present in the outgroup taxon *Orycteropus* and the archaic taxa *Arctocyon, Hyopsodus, Phenacodus,* and Mesonychidae.

The third trochanter is absent in all extant artiodactyls, and it is absent or very small in all extinct artiodactyls. Specimens of the basal artiodactyl *Diacodexis* from North America (Rose, 1985) and from Asia (Thewissen and Hussain, 1990) have a small rectangular flange on the femur that is homologous to, but smaller than, the third trochanter of *Arctocyon, Hyopsodus,* perissodactyls, and other mammals. Thus, reduction of the third trochanter is a potential synapomorphy of Artiodactyla, while complete loss of this structure is a potential synapomorphy of a higher level artiodactyl clade that includes the artiodactyl crown group. The archaic cetacean *Ambulocetus* has a third trochanter (Thewissen et al., 1996); therefore, its presence in this taxon supports the exclusion of Cetacea from the clade of all artiodactyls.

Character 156: Proximal end of astragalus (ordered).—Nearly flat to slightly concave (0); well grooved, but depth of trochlea <25% its width (1); deeply grooved, depth >30% its width (2) (derived from Schaeffer,

1947; O'Leary and Geisler, 1999). The most widely recognized character that diagnoses Artiodactyla is the double-pulleyed astragalus (Schaeffer, 1947). The "double-pulley" refers to the fact that the proximal and distal ends of the astragalus are deeply grooved, and that each end resembles a pulley. As in previous morphological studies (e.g., Thewissen and Domning, 1992; O'Leary and Geisler, 1999), the proximal and distal ends of the astragalus are treated as independent characters.

The tibial articulation surface of the astragalus is divided into two parts: (1) a medial part that faces medially or proximomedially and articulates with the medial malleolus of the tibia, and (2) a lateral part that faces proximally and articulates with the rest of the tibia. It is the second part that becomes trochleated in many mammals. In the Cretaceous eutherians *Ukhaatherium* (Horovitz, 2000), *Asioryctes* (Kielan-Jaworowska, 1977), and *Protungulatum* (Szalay and Decker, 1974), the lateral part of the tibial articular surface is slightly concave (state 0); therefore, a flat to slightly concave articulating surface on the astragalus for the tibia is probably primitive for Eutheria. In the outgroups *Orycteropus* and Leptictidae and the ungu-

late mammals *Eoconodon, Pachyaena* (fig. 4b), *Mesonyx,* and *Phenacodus* (fig. 4C: tr), the tibial articulation surface on the astragalus is well grooved. In these taxa, the maximum depth of the tibial articulation surface is less than 25% the transverse width of the trochlea, where trochlear width is measured between the medial and lateral parasagittal ridges of the tibial articulation surface (fig. 4: ltr, mtr) (state 1). The early cetacean *Ambulocetus* was also scored "1" for this character because it has a relative trochlear depth of 19% (Thewissen, 1994).

In nearly all artiodactyls, the trochlea is deeply grooved with its depth greater than 30% its width (state 2). The entire trochlea is convex along the sagittal plane but is concave in the transverse plane, thus it is shaped like a pulley (fig. 4A: tr). A deeply grooved trochlea is a potential synapomorphy of Artiodactyla; however, a few artiodactyls are coded "1" for this character. The proximal end of the astragalus is only slightly grooved in the artiodactyls *Homacodon, Merycoidodon, Leptoreodon,* and *Hexaprotodon* (state 1). The trochlea of perissodactyls is deeply grooved like most artiodactyls (state 2); however, this morphology is probably convergent because in the stem taxa to Perissodactyla (e.g., *Meniscotherium, Phenacodus*) the trochlea is slightly grooved (fig. 4C: tr).

Character 157: Astragalar canal.—Present (0); absent (1) (Shoshani, 1986). The astragalar canal perforates the proximal end of the astragalus. The proximal entrance of the canal, known as the astragalar foramen, is within or slightly plantar to the lateral tibial articulation surface, while the plantar end of the canal leads into the interarticular sulcus. Although the occupant, if any, of the astragalar canal is not known (Schaeffer, 1947), the interarticular sulcus is a point of attachment for the interosseous ligament between the astragalus and calcaneus (Sisson, 1921).
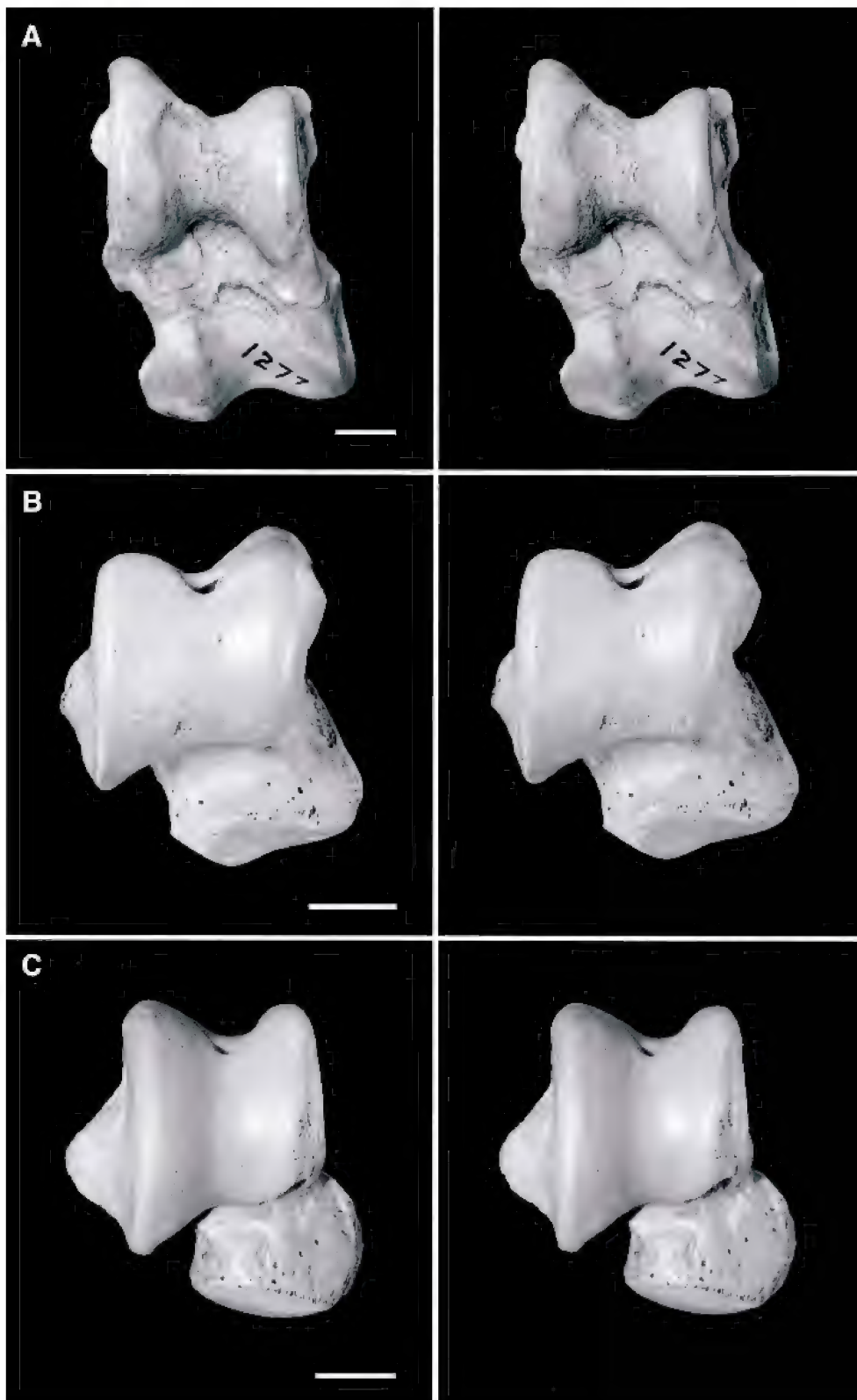
The astragalar foramen is absent in all artiodactyls, and previous authors have stated that its absence is a synapomorphy of this group (Geisler and Luo, 1998; Luckett and Hong, 1998). As can be seen in *Archaeotherium,* the trochlea of the astragalus is not perforated by an astragalar foramen (fig. 4A) (state 1). In addition, the interarticular sulcus is completely absent in *Archaeotherium* (fig.

5A), as in all other artiodactyls (Schaeffer, 1947). Many other mammals, including all perissodactyls, *Canis, Rattus,* and the mesonychids *Mesonyx* and *Synoplotherium* (Wortman, 1901), also lack an astragalar foramen. By contrast, the astragalar foramen is present in many archaic ungulates, including *Hyopsodus, Phenacodus, Meniscotherium, Pachyaena, Dissacus, Arctocyon, Eoconodon,* and *Orycteropus.* In *Pachyaena* and *Phenacodus,* the astragalar foramen is clearly visible in dorsal view (fig. 4B, C: af) (state 0).
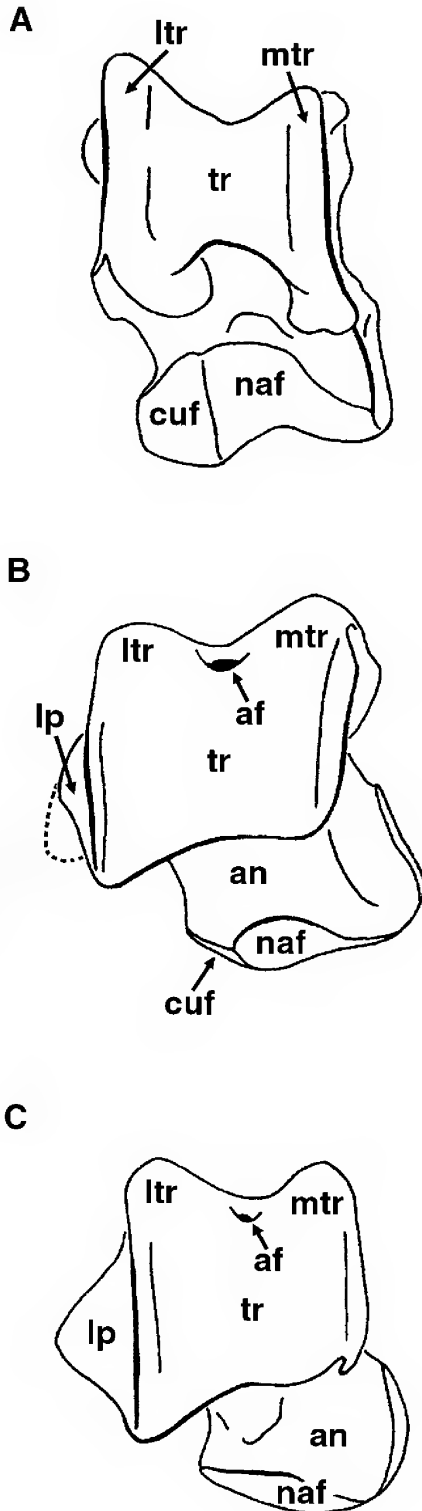
Thewissen et al. (1996) noted that the early cetacean *Ambulocetus* has an astragalar foramen; therefore, this character supports the exclusion of Cetacea from Artiodactyla (Luckett and Hong, 1998). Thewissen et al. (1998) and Thewissen and Madar (1999) described several astragali that they referred to Cetacea; however, they did not mention whether the astragalar foramen was present or absent.

Character 159: Distal end of astragalus contacts cuboid (ordered).—Contact absent (0); contact present, articulating facet on astragalus forms a steep angle with a parasagittal plane (1); contact present and large, facet almost forms a right angle with a parasagittal plane (2). In the outgroup *Orycteropus* as well as other taxa, including *Rattus, Vulpavus, Canis, Hyopsodus, Phenacodus,* and *Meniscotherium,* there is no contact between the cuboid and the astragalus. In these taxa, the head of the astragalus only contacts the navicular. In mesonychids such as *Dissacus* and *Pachyaena* (figs. 4, 5: cuf), the lateral side of the head of the astragalus bears a facet for the cuboid (state 1). The long axis of the facet is oriented anterolateral to posteromedial. In mesonychids little of the body weight bore by the astragalus could be transferred to the cuboid because their contact surfaces are oriented vertically, not transversely.

The astragali of all artiodactyls have very large cuboid facets, as is seen in *Archaeotherium* (fig. 4A: cuf). The cuboid facet is oriented nearly perpendicular to the sagittal plane, thus facing distally (state 2). A large distally facing astragalus occurs in all artiodactyls; therefore, it is a potential synapomorphy of that group. The size and orientation of the cuboid facet in artiodactyls is al-

most certainly related to distributing body weight between the third and fourth digits. The weight transferred from the astragalus to the cuboid would be passed onto the fourth digit, which is expected in a paraxonic pes such as that which occurs in all artiodactyls (Schaeffer, 1947). Paraxony of the foot and the size of the astragalus/cuboid contact are at best only partially dependent on each other because mesonychids have a paraxonic pes but only a small cuboid/astragalar contact; therefore, these characters are treated independently in the phylogenetic analysis.

Although the cuboid of early cetaceans is not known, the morphology of the putative cetacean astragali described by Thewissen et al. (1998) and Thewissen and Madar (1999) suggests that the cuboid did not contact the astragalus in these taxa. In H-GSP 97227 the neck and head of the astragalus are directed distomedially, away from the cuboid. If the cuboid was similar in size to that of mesonychids or artiodactyls, then the astragalus would not contact the cuboid. However, if the cuboid was transversely expanded, then contact was possible.

Character 162: Lateral process of astragalus.—Present, ectal facet of the astragalus faces in the plantar direction and its distal

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Fig. 4. Dorsal views of the right astragali of three ungulates. Line drawings are on page facing the stereopairs. Lateral is to the left, proximal is toward the top of the page, and the scale represent 10 mm. **A.** Right astragalus of the artiodactyl *Archaeotherium* sp. (AMNH 1277). Note the deeply grooved trochlea, absence of the lateral process, and the large cuboid facet that faces distally. This view is more accurately described as anterior because of the digitigrade posture of all artiodactyls. **B.** Right astragalus of the mesonychid *Pachyaena ossifraga* (AMNH 16154). The astragalus of *Pachyaena* has an astragalar foramen, a lateral process (broken in this specimen), and a small, distolaterally facing cuboid facet. **C.** Left astragalus (photos reversed for comparison) of *Phenacodus* sp. (AMNH 15262). Note the pronounced lateral process. Abbreviations: af, astragalar foramen; an, astragalar neck; cuf, articular facet for the cuboid; lp, lateral process; ltr, lateral trochlear ridge; mtr, medial trochlear ridge; naf, articular facet for the navicular; tr, trochlea (which is also the lateral part of the tibial articular surface).
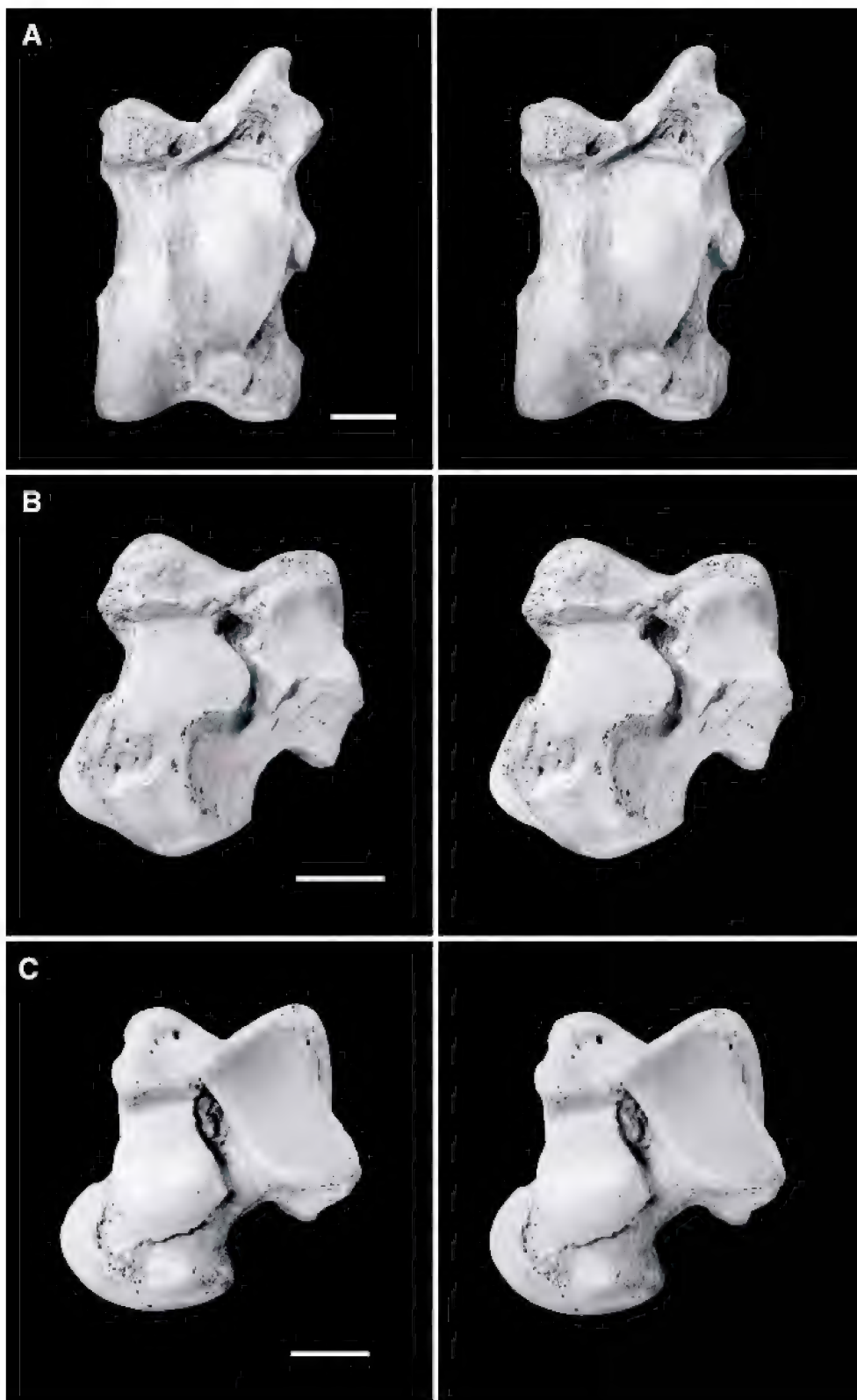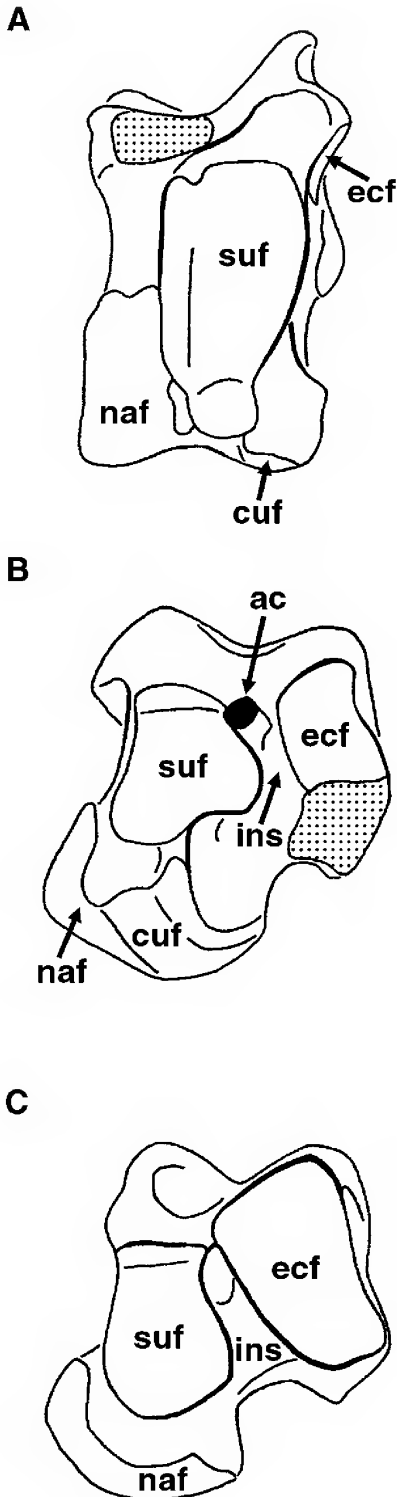
end points laterally (0); absent, ectal facet faces laterally and its long axis is parasagittal (1) (Schaeffer, 1947). The plantar face of the lateral process bears the lateral half of the ectal facet, which articulates with the lateral astragalar facet of the calcaneus. The presence or absence of the lateral process is correlated to the orientation of the ectal facet of the astragalus. If the ectal facet is oriented proximomedial to distolateral, then its distal end juts outward from the lateral side of the astragalus forming the lateral process. If the ectal facet is parasagittal in orientation, then the lateral process is absent. Schaeffer (1947) discussed the differences between the ectal facets of artiodactyls and archaic ungulates. Later, Geisler and Luo (1998) and then Thewissen and Madar (1999) used the morphology of the lateral process or ectal facet as a character for cladistic analysis. Although these authors emphasized different aspects of astragalar morphology, they are considered here to represent interdependent changes of the same morphological region.

In *Phenacodus* the ectal facet is very large and equal in width to the sustentacular facet. The ectal facet faces in the plantar direction and its long axis is oriented proximomedial

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Fig. 5. Plantar views of the right astragali of three ungulates. Line drawings are on page facing the stereopairs. Lateral is to the right, proximal is toward the top of the page, and the scale bars represent 10 mm. **A.** Plantar view of the right astragalus of the artiodactyl *Archaeotherium* sp. (AMNH 1277). Note the wide and laterally positioned sustentacular facet, absence of the interarticular sulcus, and the laterally facing ectal facet. **B.** Right astragalus of the mesonychid *Pachyaena ossifraga* (AMNH 16154). The astragalus of *Pachyaena* has a small and medially positioned sustentacular facet, an astragalar canal leading into an interarticular sulcus, and a large plantar-facing ectal facet. **C.** Left astragalus (photos reversed for comparison) of *Phenacodus* sp. (AMNH 15262). The astragalus of *Phenacodus* is very similar to that of *Pachyaena* except for an occluded astragalar canal and the absence of an articular facet with the cuboid. Abbreviations: ac, astragalar canal; cuf, articular facet for the cuboid; ecf, ectal facet; ins, interarticular sulcus; naf, articular facet for the navicular; suf, sustentacular facet.

to distolateral (fig. 5C: ecf). In association with the orientation of the ectal facet, the astragalus bears a stout, triangular-shaped lateral process (fig. 4C: lp) (state 0). The lateral side of the astragalus proximal to the lateral process is occupied by the articular surface for the lateral malleous of the fibula. The distal end of the fibular facet extends onto the lateral process, and it is twisted, relative to more proximal portions, so that it faces dorsally instead of laterally. Based on post-mortem articulation of the tibia, fibula, and astragalus in *Phenacodus* and *Pachyaena,* it appears that the lateral process in archaic ungulates forms a stop to dorsal flexion at the proximal ankle joint. Another probable function of the lateral process/ectal facet complex is in transferring weight from the astragalus to the calcaneus. When the lateral process is present, the ectal facet is perpendicular to the long axes of the tibia and fibula and thus can efficiently pass weight onto the calcaneus.

In all artiodactyls, including *Diacodexis* and *Archaeotherium* (figs. 4A, 5A), the lateral process of the astragalus is absent (state 1). Unlike *Phenacodus,* the ectal facet in artiodactyls is parasagittal and faces laterally, instead of in the plantar direction (fig. 5A: ecf). It is fairly small and could not transfer weight to the astragalus because it is parallel, not perpendicular, to the long axes of the tibia and fibula. The proximal end of the ectal facet in *Archaeotherium* does jut outward from the lateral surface of the astragalus; however, this small protrusion is not homologous to the lateral process because it is adjacent to the proximal, not the distal, end of the ectal facet.

Character 163: Sustentacular facet of the astragalus.—Narrow and medially positioned, lateral margin of sustentacular facet of the astragalus well medial to the lateral margin of the trochlea (0); wide and laterally positioned, lateral margin in line with the lateral margin of the trochlea (1) (derived from Schaeffer, 1947; Geisler and Luo, 1998). The sustentacular facet of the astragalus is the articular surface on the plantar side that articulates with the sustentaculum of the calcaneus. It is usually centered on the plantar face and is situated medial to the ectal facet. Schaeffer (1947) was the first to note that a large sustentacular facet is characteristic of

all artiodactyls. Geisler and Luo (1998) developed a cladistic character for the relative size of facet. They described state "0" as having a sustentacular width that is less than 40% the width of the astragalus and state "1" as having a sustentacular width greater than 70% that width. O'Leary and Geisler (1999) used a similar character description except that state "0" was described as being less than 50% the astragalar width.

Although not mentioned, Geisler and Luo (1998) and O'Leary and Geisler (1999) measured astragalar width across the trochlea at a position proximal to the base of the lateral process. In reviewing the coding for this character, I came upon several discrepancies. For example, both *Pachyaena* and *Phenacodus,* scored as "0" in both studies, actually fall between states "0" and "1" with sustentacular widths of 57% and 65%, respectively (fig. 5B, C: suf). Despite the similarity in size between the sustentacular facets of *Phenacodus* and *Pachyaena* and the sustentacular facets of artiodactyls, there are clear qualitative differences between them. I improved this character by emphasizing the position of the lateral margin of the sustentacular facet, instead of its relative width.

In the primitive condition, as represented by *Pachyaena* and *Phenacodus* (fig. 5B, C: suf), the lateral margin of the sustentacular facet is well medial to the lateral edge of the trochlea (state 0). In *Pachyaena ossifraga,* the sustentacular facet is kidney-shaped, with the long axis of the facet oriented proximo-laterally to distomedially (fig. 5B: suf). The sustentacular facet occupies approximately 30% of the plantar surface, and the rest of the plantar surface includes a large interarticular sulcus between the sustentacular and ectal facets and a broad rugose region between the sustentacular facet and the astragalar head.

In artiodactyls, such as *Archaeotherium* (fig. 5A: suf), the sustentacular facet is wide and is placed such that its lateral margin is in line with the lateral edge of the trochlea. Much of the apparent increase in size of the sustentacular facet is caused by the lateral position. In the primitive condition, the sustentacular facet is medial to the anterior face of the astragalar neck; therefore, a cross section through the astragalar neck is rhomboi-

dal, with much of the lateral surface visible in plantar view and much of the medial surface visible in dorsal view. The sustentacular facet appears small because the lateral surface is visible in plantar view. In artiodactyls the sustentacular facet is directly plantar to the trochlea; therefore, a cross section through the astragalus is approximately square-shaped. The lateral surface of the astragalus is not visible in plantar view, creating the appearance of a large sustentacular facet.

In addition to a far lateral position, the long axis of the artiodactyl sustentacular facet is aligned longitudinally, and thus parallel to the medial and lateral edges of the trochlea. This contrasts with the primitive condition as exemplified by *Pachyaena,* where the long axis of the sustentacular facet is oriented proximolaterally to distomedially (fig. 5B: suf). To transform the orientation of the sustentacular facet from the primitive condition to the artiodactyl morphology requires a counterclockwise (on the right astragalus) rotation of 30° to 40°. The rotation in artiodactyls coincides with expansion of the proximolateral corner of the sustentacular facet and absence of the interarticular sulcus (fig. 5A). The orientation of the sustentacular facet was not coded separately from its position because I think it is related to character 159, which codes for the size and orientation of the cuboid facet. A large cuboid facet occurs when the head of the astragalus is in a lateral position, directly distal to the trochlea. A lateral position of the astragalar head aligns the proximal and distal articulating facets of the astragalus, and the long axis of the sustentacular facet predictably stretches between the proximal and distal ends along a parasagittal line.

Thewissen et al. (1998) and Thewissen and Madar (1999) described astragali that they assigned to the basal cetacean families Ambulocetidae and Pakicetidae. Following the reasons of O'Leary and Geisler (1999), the morphology of these bones was not considered in scoring characters of the hindlimb. Although I do not reject the allocation of these isolated elements to Cetacea, I consider the association to be too weak to justify including these data in the phylogenetic analysis. Despite this uncertainty, the morphology of these astragali can be described in terms of the characters used in this study. The sustentacular facet of H-GSP 97227, a putative pakicetid astragalus, is very different from those of artiodactyls. Like *Pachyaena* and other archaic ungulates, the lateral margin of the sustentacular facet is far medial to the lateral edge of the trochlea. Unlike artiodactyls, the proximolateral corner is not expanded; however, it is unclear if the interarticular sulcus was present. I suspect it was because the cetacean *Ambulocetus* has an astragalar foramen (Thewissen et al., 1996), and in all ungulate astragali I have examined the astragalar foramen and the interarticular sulcus always coexist.

Character 165: Articulation of calcaneus and cuboid.—Flat, proximal articulating surface of the cuboid in one plane and corresponding surface of the calcaneus faces distally (0); sharply angled and curved, proximal surface of the cuboid has a distinct step between the facets for the calcaneus and astragalus (1). Although Schaeffer (1947) was the first to recognize the unique morphology of the calcaneus/cuboid contact of artiodactyls, Thewissen and Madar (1999) were the first to reformulate the character for cladistic analysis. Although Thewissen and Madar (1999) stressed the transverse widths of the articulation surfaces, I stress the angle and curvature of the facets because they are common to all artiodactyls but do not occur in any other mammal. The cuboid's articulation facet for the calcaneus in the artiodactyl *Diacodexis* (AMNH 27787) is fairly wide; therefore, a narrow facet does not characterize all artiodactyls.

In the basal eutherian *Ukhaatherium,* the cuboid facet of the calcaneus faces primarily distally, with a slight medial component (Horovitz, 2000), and a similar morphology occurs in the basal ungulate *Protungulatum* (Szalay and Decker, 1974). Thus, the probable primitive condition for Eutheria is a cuboid facet that faces distally or distomedially (state 0). The primitive morphology of the calcaneus/cuboid joint is exemplified by the mesonychid *Pachyaena* (fig. 6B: caf). The articular surface on the cuboid for the calcaneus is nearly flat and approximately triangular in shape. Lateral to the articular surface for the calcaneus is a rectangular con-
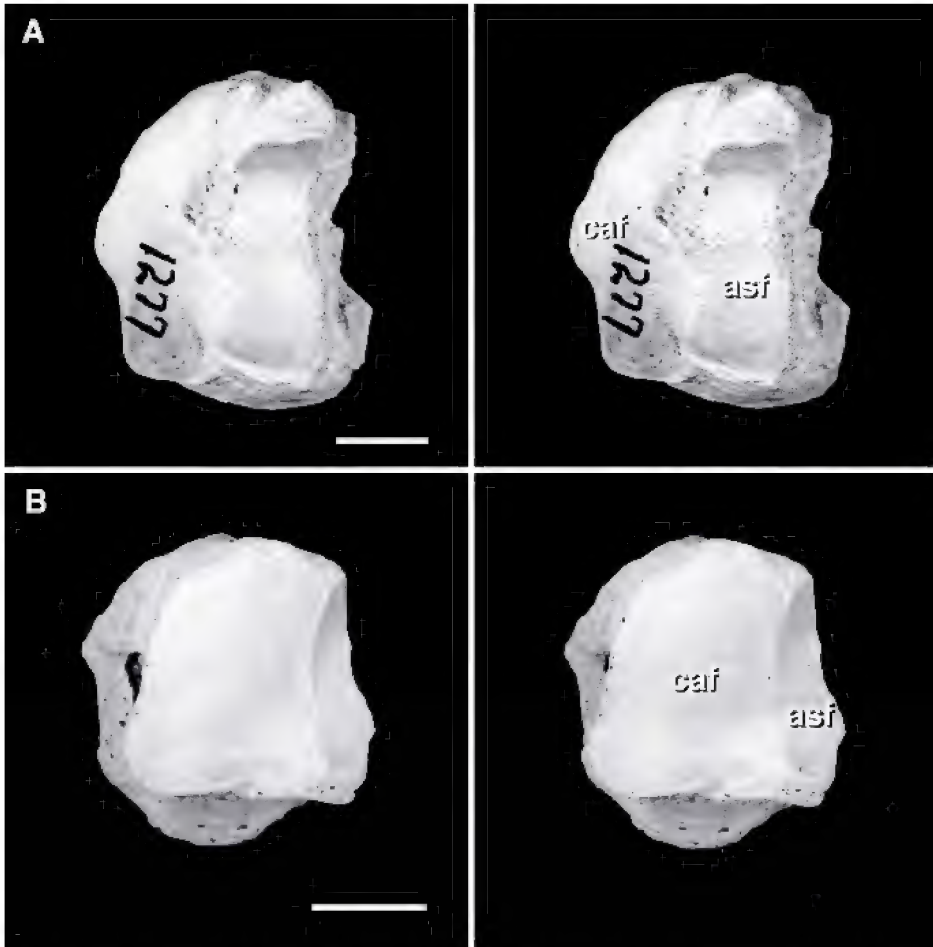
Fig. 6.   Proximal views of the cuboids of *Archaeotherium* and *Pachyaena,* with right and left stereopair views. Plantar is toward the top of the page, lateral is to the left, and the scale bars represent 10 mm. **A.** Right cuboid of the artiodactyl *Archaeotherium* (AMNH 1277). Note the distinct step between the articular facets for the astragalus and cuboid, a morphology common to all artiodactyls. **B.** Right cuboid of *Pachyaena ossifraga* (AMNH 16154). Note the wide articular facet for the cuboid. Abbreviations: asf, articular facet for the astragalus; caf, articular facet for the calcaneus.

cave facet for the astragalus (fig. 6B: asf). Both the calcaneus facet and the astragalar facet of the cuboid are nearly in the same plane transverse plane (fig. 7B), and the joints between the cuboid and the astragalus and calcaneus are collectively referred to as the lower tarsal joint. During movement at the lower tarsal joint, the tuber of the calcaneus would have maintained a similar angle with the pes because the joint surface is fairly flat.

In nearly all artiodactyls the articulation between the calcaneus and the cuboid is transversely narrow (fig. 6A: caf). The narrowness of the joint is correlated with the degree of alignment of the astragalar head, a character not included because of its probable interdependence with this and other ankle characters. Near or total longitudinal alignment of the astragalar head with the trochlea of the astragalus is correlated with a large cuboid/astragalus contact, and consequently with a narrower calcaneus/cuboid contact. The correlation is not perfect, as is shown by *Diacodexis* (AMNH 27877). In this specimen, the calcaneus facet on the cuboid is still large even though the cuboid has substantial contact with the astragalus. The calcaneus
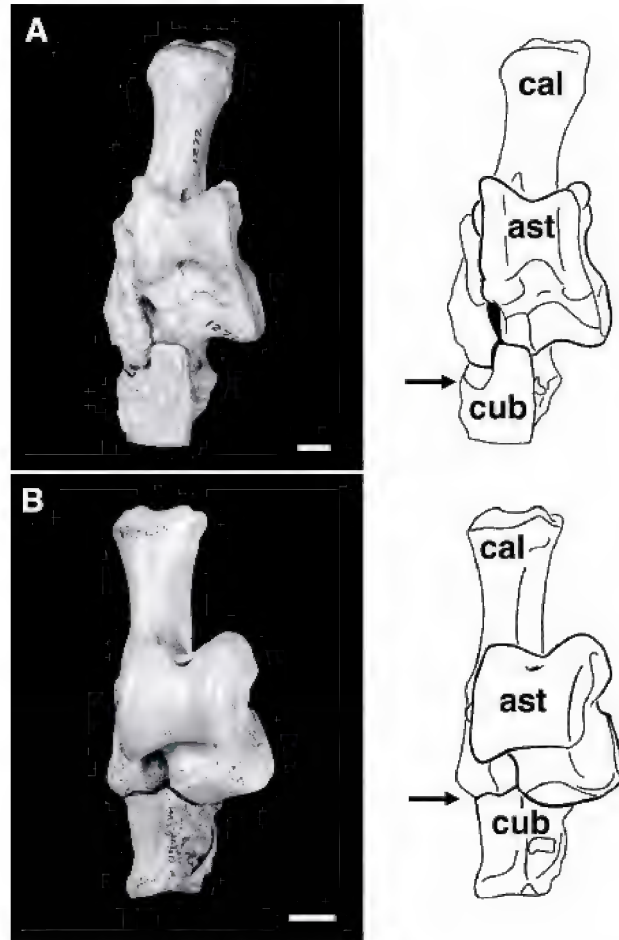
Fig. 7. Dorsal views of the right ankles of two ungulates. Lateral is to the left, proximal is toward the top of the page, and the scale bars represent 10 mm. Arrows indicate the dorsal edge of the cuboid's articular facet for the calcaneus. **A.** Ankle of *Archaeotherium* (AMNH 1277). Note the distinct step between the articulation of the cuboid with the calcaneus and its articulation with the astragalus. The calcaneus will move farther down the face of the cuboid during dorsal flexion. **B.** Ankle of *Pachyaena ossifraga* (AMNH 16154). Note that the cuboid articulates with the calcaneus and the astragalus in nearly the same transverse plane. Abbreviations: ast, astragalus; cal, calcaneus; cub, cuboid.

facet is wide and its lateral edge overhangs more distal parts of the cuboid.

The cuboid of artiodactyls can be distinguished from all other mammals because there is a pronounced step between the dorsal (anterior if digitigrade) edges of the cuboid articulation surfaces for the astragalus and calcaneus (figs. 6A, 7A). The articulating facet for the astragalus is more proximal than that for the calcaneus. Two factors apparently contribute to the formation of the step: (1) the convexity of the articulating surface with the calcaneus, and (2) a relatively short neck

for the astragalus. The cuboid's facet for the calcaneus is convex parasagittally, while its facet for the astragalus is concave parasagitally (fig. 6A). The curve in the calcaneus facet is largely formed by a distal turn near the dorsal edge of the facet, which accentuates the step between the cuboid and astragalar facets. In addition, the neck of the astragalus in artiodactyls appears to be shorter than those of archaic ungulates; therefore, the astragalar facet on the cuboid is in a more proximal position.

According to Schaeffer (1947), the angle

between the calcaneus and the pes in artio-
dactyls changes during movement at the low-
er tarsal joint, thus indicating rotation be-
tween the cuboid and calcaneus. The axis of
rotation for movement at the calcaneus/cu-
boid joint is nearly transverse, perpendicular
to the lateral side of the cuboid, and passes
through the proximal end of the cuboid and
the distal end of the astragalus. To maintain
continual contact between the calcaneus and
cuboid during movement at the lower tarsal
joint, the astragalus and calcaneus must
move simultaneously in the same direction.
This suggests that the curved cuboid/calca-
neus articulation allows for a larger amount
of rotation between the astragalus and the na-
vicular than in taxa that have a flat calcaneus/
cuboid articulation. The amount of rotation
is not directly proportional, with the astrag-
alus rotating much more than the calcaneus.

PHYLOGENETIC ANALYSES AND OPTIMIZATIONS

Parsimony-based cladistic methods were
used for phylogeny reconstruction, resulting
in phylogenetic hypotheses that maximize
explanatory power (Farris, 1983). MacClade
3.01 (Maddison and Maddison, 1992) was
used for entering and editing the morpholog-
ical matrix, and NONA 1.9 (Goloboff, 1994)
and PAUP 3.1.1 (Swofford, 1993) were used
for finding the most parsimonious (MP)
trees. Tree searches with PAUP were heuris-
tic with the following parameters: TBR (tree
bisection and reconnection) branch swap-
ping, hold 1 tree at each step, save no more
than 10 suboptimal trees for each replicate,
and random stepwise addition of taxa with
1000 replications. Two separate searches
with NONA were performed with the follow-
ing commands: (1) hold/10 and mult*1000;
(2) nix* 10000, with the starting tree from
the first analysis. The first analysis is com-
parable to that of PAUP, and the second uses
the parsimony ratchet, a method of reweight-
ing characters to explore different tree is-
lands (Nixon, 1999). Comparisons between
different optimizations and tree-length cal-
culations for alternative topologies were per-
formed using MacClade 3.01 (Maddison and
Maddison, 1992). Unequivocal synapomor-
phies were derived using the apo/ command
in NONA. Citations are provided where un-

equivocal synapomorphies, as indicated in
this analysis, have previously been suggested
as synapomorphies of the same clade. The
term "unequivocal", as used here, means
that the character change occurs at a specific
node in all most parsimonious trees under all
most parsimonious optimizations.

Previous phylogenetic hypotheses were
tested with the morphological matrix of this
study by calculating their minimal tree
lengths. Many of the taxa that are included
here were not included by previous authors.
Newly added taxa were incorporated into
their hypotheses by using a backbone phy-
logenetic constraint, which when enforced in
a search places taxa that are excluded from
the constraint definition so that the overall
tree length is minimized (Swofford and Be-
gle, 1993). Constraint trees were constructed
in MacClade 3.01 and then implemented in
PAUP 3.1.1 by saving the shortest trees that
were compatible with the constraint. The
length of the unconstrained most parsimoni-
ous trees was subtracted from the length of
the shortest trees from the constrained anal-
yses to calculate the degree, measured in
number of steps, that the current matrix con-
tradicts alternative phylogenetic hypotheses.

BRANCH SUPPORT

Branch support (Bremer, 1988, 1994) was
determined by combining the results of sev-
eral separate analyses. The first analysis used
extensive swapping on trees found by 100
random addition searches, as implemented in
NONA (Goloboff, 1994). More than 100,000
trees were found within 10 steps of the op-
timal length. Strict consensus trees for all
trees less than a specific length were con-
structed to determine the branch-support val-
ues for each clade. Available computer mem-
ory filled before all branch swapping was
performed on all trees; therefore, I suspect
that some of the initial branch-support values
were overestimated. To improve the estimate,
two additional tree searches using the parsi-
mony ratchet (Nixon, 1999), as implemented
in NONA, were used to first find all trees that
were one step longer and then all trees that
were two steps longer. Swapping was per-
formed on all trees before the memory filled;
therefore, nodes with branch-support values

reported in figure 8 of 1 or 2 are thought to be accurate.

The branch-support values greater than 2 were checked with PAUP (Swofford, 1993) by finding the shortest trees that are not compatible with a constraint tree, where the constraint specifies one node in the strict consensus of the most parsimonious trees. Constraint trees, command files, and output files were generated using the program TreeRot (Sorenson, 1996). The command file generated by TreeRot was modified so that 100 heuristic replicates were performed for each node and only 20 suboptimal trees were held for each replicate. The lowest branch-support value over all analyses was chosen as the final estimate. This multiple-step approach resulted in a decrease in one to three steps for branch support values of several nodes, as compared to the initial estimate from the 100,000 saved trees. Bootstrapping was not used as a measure of character-based nodal support because it violates the basic assumptions of the method when applied to character data (Kluge and Wolf, 1993; Carpenter, 1996). The character matrix used in this study is not a random sample of characters, but was compiled by focusing on characters relevant to the higher level phylogeny of Artiodactyla, Cetacea, and Mesonychidae.

RESULTS

ALL TAXA

When all ingroup and outgroup taxa were included, both PAUP and NONA found 32 most parsimonious trees that were 1635 steps long. When all polymorphism was interpreted as uncertainty, the tree length was 1412 steps. The default in NONA reported 22 trees, but 32 trees were found when the amb= command was used. The difference relates to how the programs deal with zero-length branches, as discussed by Coddington and Scharff (1994). When using the parsimony ratchet (Nixon, 1998), as implemented in NONA, the same 32 shortest tree were found in over 60% of 10,000 iterations. A strict consensus of the 32 most parsimonious trees includes a monophyletic Perissodactyla, Artiodactyla, Paraxonia (Artiodactyla + Cetacea + Mesonychidae + Hapalodectidae), Hippopotamidae, Oreodontoidea, Neoselen-

odontia, Ruminantia, Cameloidea (Camelidae + Oromerycidae), Camelidae, Xiphodontoidea, and Cetacea (figs. 8, 9). Suina (Suidae + Tayassuidae) and Suoidea (Suina + Hippopotamidae) are monophyletic only if *Perchoerus,* which has been considered a basal peccary, is excluded from both groups. *Phenacodus* and *Meniscotherium* are successive sister groups to Perissodactyla in all most parsimonious trees, as suggested by previous authors (Gregory, 1910; Radinsky, 1966; Van Valen, 1978; Thewissen and Domning, 1992; Geisler and Luo, 1998; O'Leary and Geisler, 1999).

A monophyletic Artiodactyla (fig. 8: taxon A) was found in all most parsimonious trees and has a branch support of two. Monophyly of Artiodactyla is breached in trees three steps longer by the inclusion of Perissodactyla, but not Cetacea, into the clade including all artiodactyls. Four unequivocal synapomorphies support Artiodactyla, including characters 36 ($2 \rightarrow 1$), a short mastoid process of the petrosal; 49 ($1 \rightarrow 0$), absence of alisphenoid canal (O'Leary and Geisler, 1999); 96 ($0 \rightarrow 1$), presence of an entocingulum on P^4 (fig. 2A: en); and 124 ($0 \rightarrow 1$), presence of a transverse ridge of the occipital condyle dividing it into dorsal and ventral halves (fig. 3: or). Several characters that have been considered as synapomorphies of Artiodactyla are equivocal when optimized onto these trees because *Andrewsarchus,* a poorly known taxon that is coded for only 39% of the characters, is positioned as its sister group. The following characters are synapomorphies of Artiodactyla under delayed optimization or for Artiodactyla + *Andrewsarchus* under accelerated optimization: characters 135 ($0 \rightarrow 1$), absence of entepicondylar foramen of the humerus; 152 ($0 \rightarrow 1$), reduced third trochanter of the femur (Luckett and Hong, 1998; O'Leary and Geisler, 1999); 156 ($1 \rightarrow 2$), deeply grooved, tibial articular surface of the astragalus (Schaeffer, 1947); 157 ($1 \rightarrow 0$), absence of the astragalar canal (Luckett and Hong, 1998; Geisler and Luo, 1998); 159 ($1 \rightarrow 2$), astragalar contact with cuboid large and oriented nearly perpendicular to the sagittal plane; 162 ($0 \rightarrow 1$), absence of lateral process of astragalus (Schaeffer, 1947; O'Leary and Geisler, 1999; Thewissen and Madar, 1999);
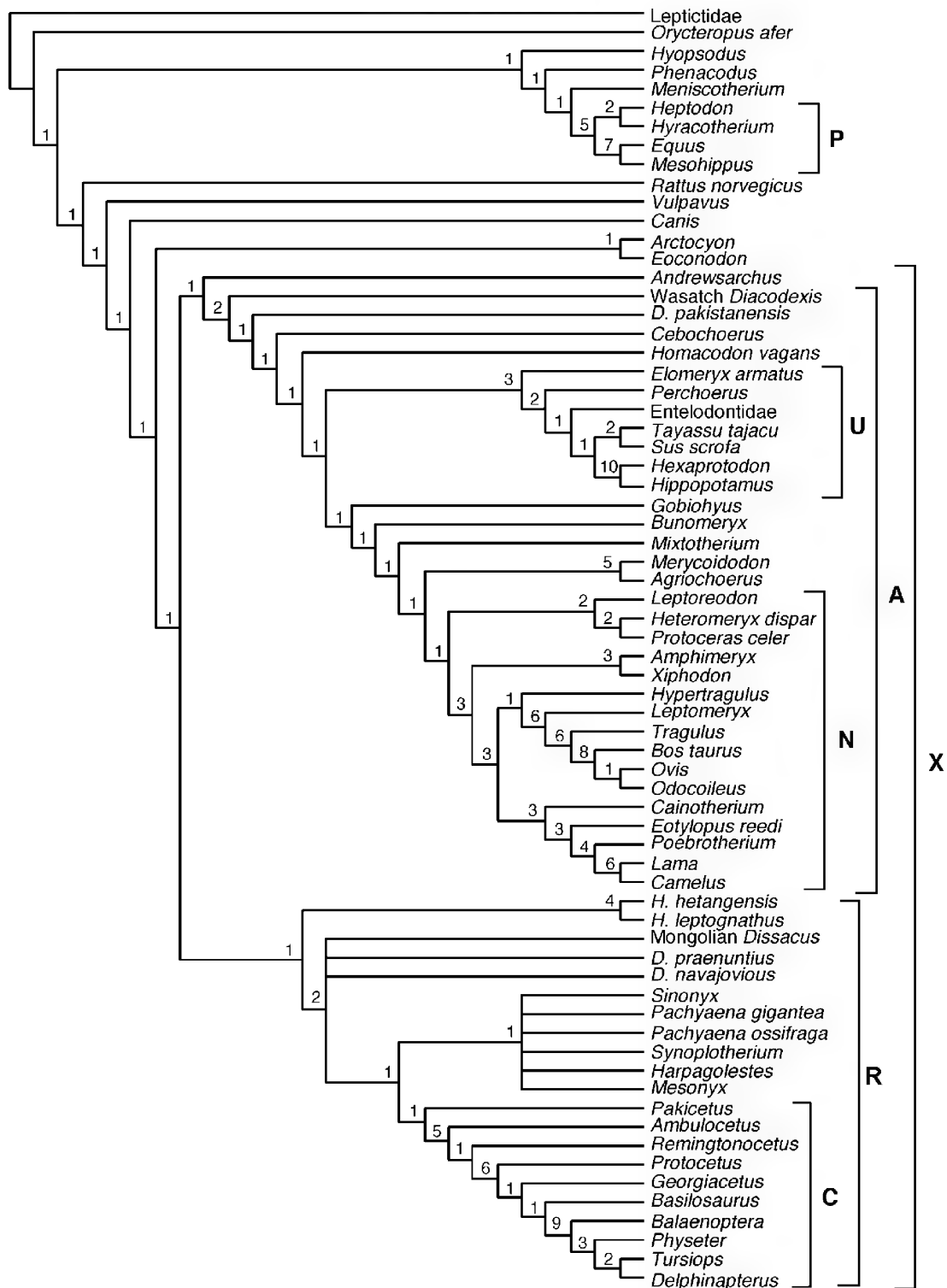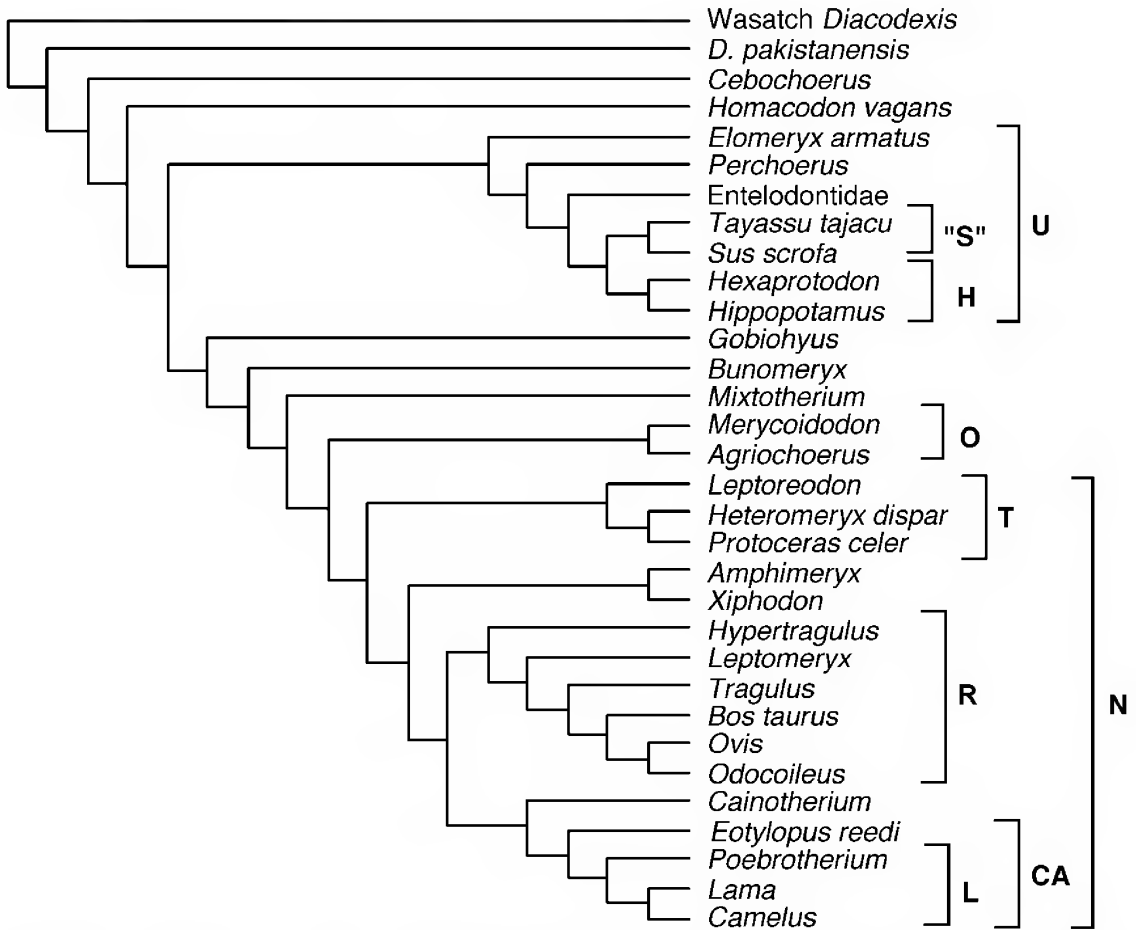
Fig. 9. The phylogeny within Artiodactyla, enlarged from the strict consensus shown in figure 8. Ruminantia is monophyletic in all most parsimonious trees as well as the superfamilies or families Cameloidea, Camelidae, Oreodontoidea, Protoceratidae, and Hippopotamidae. Taxon abbreviations: CA, Cameloidea; H, Hippopotamidae; L, Camelidae; N, Neoselenodontia; O, Oreodontoidea; R, Ruminantia; "S", Suina, which is paraphyletic because it excludes *Perchoerus*; T, Protoceratidae; U, Suiformes.

163 (0 → 1), laterally positioned sustentacular facet (Schaeffer, 1947; Geisler and Luo, 1998; Thewissen and Madar, 1999; O'Leary and Geisler, 1999); 165 (0 → 1), transversely narrow and sharply angled cuboid/calcaneus articulation (Thewissen and Madar, 1999); and 175 (0 → 1), long third metatarsal. Absence of the alisphenoid canal (Geisler and Luo, 1998) and probably absence of the lateral process of the astragalus (Thewissen et al., 1998; Thewissen and Madar, 1999) also occur in cetaceans.

←

Fig. 8. Strict consensus of 32 most parsimonious trees for the morphological data listed in appendix 3. Each most parsimonious tree is 1635 steps long (polymorphisms included as steps), has a consistency index of 0.31, and has a retention index of 0.60. Branch-support values are immediately above and to the left of their respective nodes. Artiodactyla, Neoselenodontia, and Suiformes are monophyletic in all shortest trees. Taxon abbreviations: A, Artiodactyla; C, Cetacea; N, Neoselenodontia, P, Perissodactyla; R, Acreodi; U, Suiformes; X, Paraxonia.

Several characters previously suggested as synapomorphies of Artiodactyla are considered equivocal synapomorphies in this analysis because they may support other nodes, and others are precluded from being artiodactyl synapomorphies because of their absence in many basal artiodactyls. An enlarged lacrimal (states 3 and 4 of character 60) is not a synapomorphy of Artiodactyla, as suggested by Prothero (1993), because the lacrimal is small, relative to the orbit, in *Diacodexis pakistanensis, Gobiohyus, Mixtotherium, Cebochoerus,* camels, basal ruminants, *Cainotherium,* and *Agriochoerus.* Based on the most parsimonious trees for the morphological data described here, an enlarged lacrimal is interpreted to have evolved twice, being a synapomorphy of Suiformes (figs. 8, 9: taxon U) and of the clade including *Tragulus, Ovis, Bos,* and *Odocoileus.* An enlarged orbitosphenoid separating the frontal and alisphenoid was also mentioned by Prothero (1993) as an artiodactyl synapomorphy (character 51); however, the alisphenoid contacts the frontal in *Diacodexis pakistanensis,* Entelodontidae, and *Perchoerus.* Separation of the frontal and alisphenoid by the orbitosphenoid is instead interpreted as a synapomorphy of a subclade of artiodactyls that includes *Bunomeryx,* Oreodontoidea, and Neoselenodontia. A trochleated distal articular surface for the navicular on the astragalus has been suggested as an artiodactyl synapomorphy (Schaeffer, 1947); however, the surface in *Diacodexis* is slightly grooved, similar to the degree seen in perissodactyls and mesonychids. A trilobed dP_4 is a synapomorphy of the crown group of artiodactyls and possibly of the entire group (Gentry and Hooker, 1988; Luckett and Hong, 1998). *Diacodexis* and *Homacodon* are scored as "?" for this character; however, a potentially homologous and early stage of this morphology has been reported in some specimens of *Diacodexis* (Luckett and Hong, 1998).

Paraxonia (fig. 8: taxon X), a clade including Artiodactyla and Cetacea to the exclusion of Perissodactyla, was present in all most parsimonious trees. This result is consistent with recent parsimony-based morphological analyses (Geisler and Luo, 1998; O'Leary and Geisler, 1999) but is unlike earlier studies that found a closer phylogenetic relationship between Cetacea and Perissodactyla (Novacek, 1986; Novacek and Wyss, 1986; Prothero et al., 1988; Thewissen, 1994). Paraxonia has a branch support of only one but is supported by several postcranial characters, including characters 139 (0 → 2), posterior edge of ulna concave; 141 (0 → 3), proximal end of radius split into three articulation surfaces; 142 (0 → 1), distal radius split into scaphoid and lunate fossae; 158 (0 → 1), saddle-shaped navicular articulation surface on the astragalus (O'Leary and Geisler, 1999); and 179 (0 → 1), ventral edge of distal phalanges flat (O'Leary and Geisler, 1999). Three characters listed by Geisler and Luo (1998) as unequivocal synapomorphies of Paraxonia are here considered equivocal: reduced entepicondyle of humerus, three primary bronchi of the lungs, and sparse cavernous tissue of the penis. As the name Paraxonia implies, a paraxonic hindlimb has been previously considered a potential synapomorphy of this clade (Thewissen, 1994; Geisler and Luo, 1998); however, this character state is here optimized as a synapomorphy of a more inclusive group that includes *Arctocyon* and carnivores. *Canis* clearly has a paraxonic pes (Evans, 1993: fig. 10–115), and *Vulpavus* (AMNH 12626) has a slightly paraxonic pes comparable to the condition seen in mesonychids (O'Leary and Rose, 1995b).

All of the most parsimonious trees include several clades of suiform artiodactyls that contradict the molecule-based phylogenies that place Hippopotamidae as a close relative of ruminants and cetaceans. Suiformes (figs. 8, 9: taxon U), here defined as Hippopotamidae + Suidae + Tayassuidae + Entelodontidae + Anthracotheriidae, has a branch support of three and is diagnosed by 11 unequivocal synapomorphies: characters 2 (0 → 1), absence of sulcus on promontorium for the internal carotid artery; 7 (0 → 1), small postglenoid foramen; 8 (0 → 1), postglenoid foramen in petrosal/squamosal suture; 11 (0 → 1), absence of subarcuate fossa of the petrosal; 36 (1 → 0), absence of mastoid process of the petrosal; 40 (0 → 2 or 3), external auditory meatus of intermediate length or long; 60 (1 → 2 or 3), lacrimal exposure on face moderate or large; 64 (0 → 1), elongate

face; 73 (0 → 1), angle of mandible forms a ventral flange; 91 (0 → 1), P¹ with two roots; and 137 (0 → 1), humerus bears intercondylar ridge. If *Perchoerus* is excluded from Suina (fig. 9: taxon ''S''), then Suina has a branch support of three. In addition, seven character states are optimized to have evolved at this node, including characters 25 (1 → 0), contact between exoccipital and ectotympanic bulla absent; 57 (2 → 3), anterior edge of orbit over M³; 65 (1 → 0), anterior opening of infraorbital canal between M¹ and P⁴, 66 (0 → 1), lateral surface of maxilla is highly concave; 95 (0 → 1), P⁴ metacone present; 96 (1 → 0), P⁴ entocingulum absent; and 176 (1 → 2), distal ends of metapodials have keels that wrap around onto their anterior sides.

Camelidae, Ruminantia, and extinct relatives form several clades in all most parsimonious trees to the exclusion of Hippopotamidae, Suidae, and Tayassuidae. Neoselenodontia has a branch support of one (figs. 8, 9: clade N) and is supported by six unequivocal synapomorphies: characters 35 (0 → 1), anterior wall of facial nerve sulcus formed by ectotympanic bulla; 133 (0 → 1), small supraspinatus fossa on the scapula; 154 (0 → 1), tibia and fibula fused at proximal ends; 161 (1 → 0) lateral surface of proximal half of astragalus is concave; 172 (1 → 3), middle portion of second metatarsal absent; and 174 (1 → 3), middle portion of fifth metatarsal absent. Webb and Taylor (1980) listed the fusion of the ectocuneiform with the mesocuneiform as a synapomorphy of Neoselenodontia. However, the fusion also occurs in *Merycoidodon* and *Agriochoerus,* and it therefore supports a larger clade including Neoselenodontia and Oreodontoidea. Within Neoselenodontia is a clade that includes Camelidae, Ruminantia, Xiphodontoidea, Oromerycidae, and *Cainotherium* but excludes Protoceratidae. This clade has a branch support of three and is diagnosed by four unequivocal synapomorphies, including characters 23 (0 → 1), stylohyoid oriented anteroventrally; 62 (0 → 1), presence of a fenestra at the junction of the lacrimal, maxilla, and frontal; 103 (0 → 1) M³ and M² subequal; and 140 (0 → 1 or 2), radius and ulna partially or completely fused.

Acreodi (Hapalodectidae + Mesonychidae + Cetacea) has a branch support of one (fig. 8: taxon R) and is supported by eight unequivocal synapomorphies: characters 70 (0 → 1), embrasure pits on the palate present; 99 (1 → 2), strong parastyle on M¹; 101 (0 → 1), M² metacone half the size of the paracone; 110 (0 → 2), paraconule absent (O'Leary, 1998a); 115 (0 → 1), lower molar paraconid or paracristid directly anterior to protoconid; 116 (0 → 2), hypoconulid on M₃ absent (Thewissen, 1994; O'Leary, 1998a; Geisler and Luo, 1998); 120 (0 → 1), lower molar protoconids approximately twice the height of molar hypoconids (Prothero et al., 1988); and 123 (0 → 1), talonid basins narrow transversely with hypoconids centered on the teeth (Thewissen, 1994; O'Leary, 1998a; Geisler and Luo, 1998). The clade including Mesonychidae and Cetacea but excluding Hapalodectidae has a branch support of two and is diagnosed by three unequivocal synapomorphies: characters 7 (0 → 1), small postglenoid foramen; 45 (1 → 0), foramen ovale anterior to glenoid fossa (Geisler and Luo, 1998); and 111 (1 → 2), only one cusp in the posterolingual quadrant of the upper molars. Unlike O'Leary (1998a), but similar to Geisler and Luo (1998) and Luo and Gingerich (1999), *Hapalodectes* is the sister group to a clade that includes Cetacea and mesonychids. Luo and Gingerich (1999) listed several basicranial characters that unite mesonychids and cetaceans. One of these, enlargement of the tegmen tympani, is interpreted here as an equivocal synapomorphy of Acreodi because it cannot be scored in *Hapalodectes.* Their character 37, shape of the external auditory meatus, is split into two characters: character 39, angle of the mastoid process of the petrosal, and character 40, length of external auditory meatus. An elongate external auditory meatus supports a clade that includes derived mesonychids (i.e., *Sinonyx, Pachyaena, Mesonyx*) and cetaceans but excludes *Dissacus.* A sharp angle for the mastoid process of the petrosal is an equivocal synapomorphy of Acreodi.

Unlike several previous morphological studies (O'Leary, 1998a; Geisler and Luo, 1998; Luo and Gingerich, 1999), Mesonychidae was not monophyletic in the most parsimonious trees for this matrix. Instead, the early mesonychid *Dissacus* was the sister

group to a clade including Cetacea plus all other mesonychids. The clade of Cetacea and all mesonychids except *Dissacus* has a branch support of one and is diagnosed by two unambiguous synapomorphies: characters 40 ($2 \rightarrow 3$), long external auditory meatus on the squamosal, and 102 ($0 \rightarrow 1$), M_1 metaconid absent or forms a slight lingual swelling on the protoconid.

Cetacea (fig. 8: clade C) has a relatively high branch support of seven and is diagnosed by 15 unequivocal synapomorphies: characters 4 ($0 \rightarrow 1$), sulcus for proximal stapedial artery absent (O'Leary and Geisler, 1999); 10 ($0 \rightarrow 1$), posttemporal canal absent; 14 ($1 \rightarrow 2$), fossa for tensor tympani muscle forms a circular pit with an anterior groove; 19 ($0 \rightarrow 1$), pachyosteosclerotic bulla (Thewissen, 1994; Luo, 1998; Luo and Gingerich, 1999; O'Leary and Geisler, 1999); 24 ($0 \rightarrow 1$), bulla articulates with the squamosal via a circular entoglenoid process (Luo and Gingerich, 1999; O'Leary and Geisler, 1999); 38 ($0 \rightarrow 1$), mastoid process of petrosal not exposed posteriorly (O'Leary and Geisler, 1999); 44 ($1 \rightarrow 0$), preglenoid process absent; 49 ($1 \rightarrow 0$), alisphenoid canal absent (O'Leary and Geisler, 1999); 93 ($0 \rightarrow 1$), P^4 protocone absent (O'Leary, 1998a; O'Leary and Geisler, 1999); 94 ($0 \rightarrow 1$), P^4 paracone greater than twice the height of M^1 paracone (Thewissen, 1994; O'Leary, 1998a; O'Leary and Geisler, 1999); 95 ($1 \rightarrow 0$), P^4 metacone absent, 99 ($2 \rightarrow 0$ or 1), M^1 parastyle weak or absent; 103 ($2 \rightarrow 1$), M^3 and M^2 subequal; 114 ($0 \rightarrow 1$), lingual cingulid on lower molars present (O'Leary, 1998a; O'Leary and Geisler, 1999); and 122 ($1 \rightarrow 2$ to 0), reentrant groove on lower molars absent or on mesial side of tooth.

EXTANT TAXA ONLY

If the matrix is analyzed with all extinct taxa deleted, the result is two most parsimonious trees of 587 steps long (length includes polymorphisms). Several groups are common to both most parsimonious trees, including Ruminantia, Camelidae, Neoselenodontia, Hippopotamidae, Cetacea, and Odontoceti. The only difference between the two trees is the position of *Tayassu*. In one tree it is the sister group to *Sus* (fig. 10A), while

in the other it is the sister group to a clade that includes *Equus* and Neoselenodontia. The inclusion of *Equus* within the artiodactyl clade as the sister group to Neoselenodontia renders Artiodactyla paraphyletic; however, Cetacea is excluded from the artiodactyl clade, as in the analysis including both extant and extinct taxa. Suoidea is paraphyletic in both most parsimonious trees with Hippopotamidae as the sister group to all other artiodactyls and *Equus*.

TESTING OTHER PHYLOGENIES

As a whole and on a clade-by-clade basis, the controversial molecule-based phylogeny (e.g., Gatesy et al., 1999b) that places Cetacea within three artiodactyl clades is strongly contradicted by the morphological data presented by this study. The shortest morphology-based tree that has a monophyletic Whippomorpha is 1642 steps, or 7 steps longer than the shortest trees (fig. 11: clade W). A monophyletic Cetruminantia occurs in trees 23 steps longer (fig. 11: clade CR), and Artiofabula occurs in trees 18 steps longer (fig. 11: clade AF). The shortest morphology-based tree that includes all of these clades and is fully compatible with the most parsimonious trees of Gatesy et al., (1999b) has 1660 steps, or 25 steps longer than the length of the unconstrained most parsimonious trees. The shortest tree that is also compatible with the most parsimonious trees of O'Leary and Geisler (1999) is 1674 steps (fig. 1A), much longer than the molecule-based topology. This result is not surprising because the constraint based on O'Leary and Geisler's (1999) study specifies the position of 39 taxa, while the molecule-based constraint only specifies the position of 17.

DISCUSSION

ARTIODACTYL MONOPHYLY

As in the studies of Geisler and Luo (1998) and O'Leary and Geisler (1999), Artiodactyla was monophyletic in all shortest trees, even though cetaceans are not scored for several postcranial characters that support artiodactyl monophyly (fig. 8: taxon A). Forcing Cetacea, but not mesonychids, to a topological position inside Artiodactyla re-
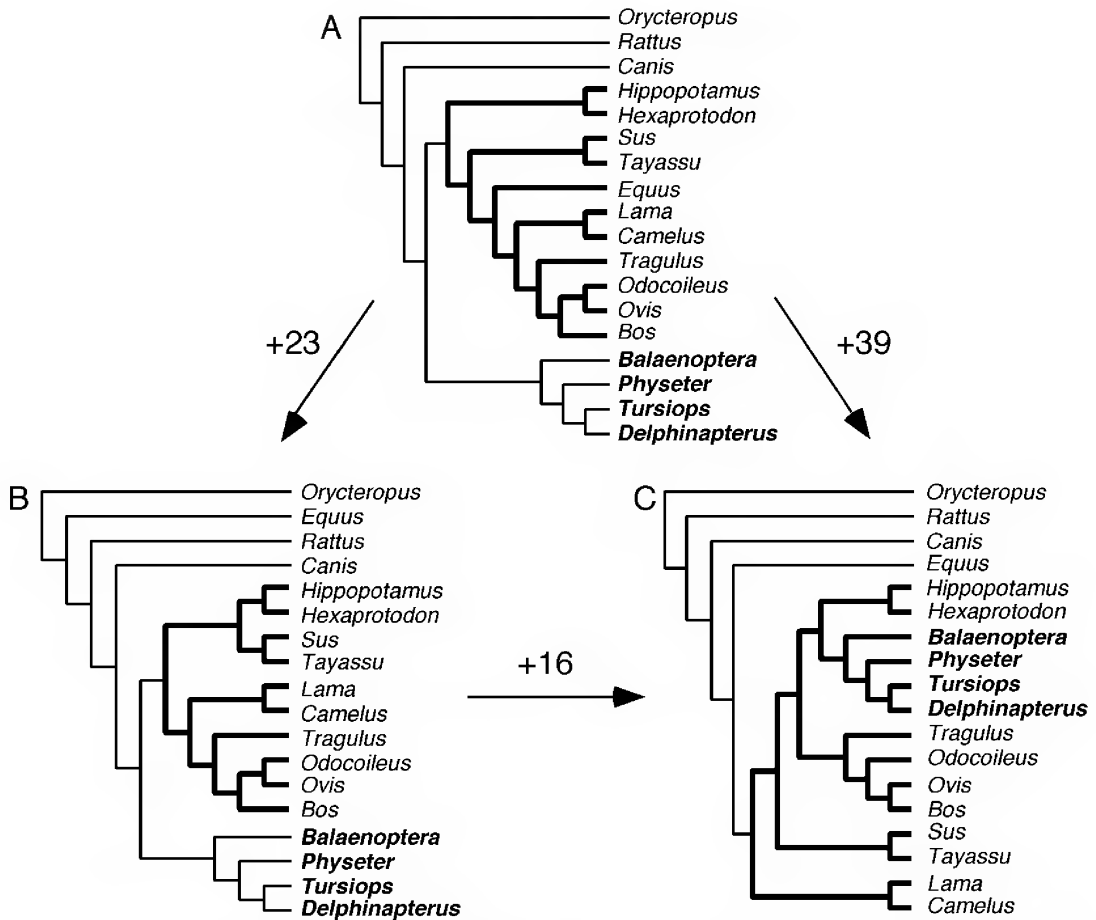
Fig. 10.   **A.** One of two most parsimonious trees based on the morphological data in appendix 3, if all extinct taxa and their character codings are excluded from the phylogenetic analysis. *Sus* and *Tayassu* do not form a clade in the other shortest tree; instead, *Tayassu* is the sister group to Neoselenodontia and *Equus*. Tree A has a length of 483 steps. **B.** The most parsimonious tree based on all data in appendix 3; unlike tree A, all taxa were included in the analysis (see fig. 8). The extinct taxa were pruned from the tree in fig. 8 to produce tree B, and the length was recalculated as 490 steps with all extinct taxa and their codings removed. **C.** The most parsimonious tree from the WHIPPO-2 matrix of Gatesy et al. (1999a); by using the data for extant taxa only in appendix 3, the tree length is 499 steps. Unlike O'Leary and Geisler (1999), if all extinct taxa are excluded, the most parsimonious trees still exclude Cetacea from the clade including all extant artiodactyls (tree A). Even though the topology of the most parsimonious tree for the morphology matrix does not have a monophyletic Artiodactyla (tree A), the hypothesis based on all taxa (tree B) is still more parsimonious than a molecule-based hypothesis (tree C) by 16 steps. Bold branches in trees denote the clade that includes all extant artiodactyls; taxa in bold are extant cetaceans. Cetacea is excluded from the artiodactyl clade in trees A and B, while it is included within the artiodactyl clade in tree C.

quires that most of the dental and basicranial similarities between mesonychids and cetaceans be reinterpreted as convergence. If both cetaceans and mesonychids are placed inside Artiodactyla, then several of the postcranial characters that support artiodactyl monophyly must have reversed. Either way,

placing cetaceans and mesonychids as a clade outside of Artiodactyla leads to shorter morphology-based trees. Even though the postcrania of the early cetacean *Ambulocetus* are only partially known, like mesonychids it differs from all extant artiodactyls in the following characters: centrale bone in the
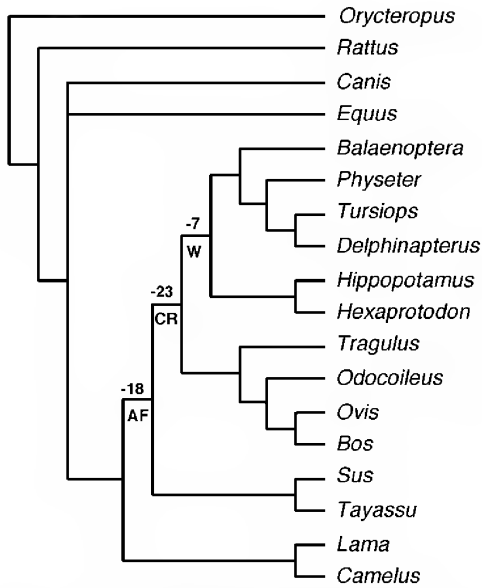
Fig. 11.   The molecule-based tree from Gatesy et al. (1999a) with the degree (number of steps) that the data in appendix 3 contradict phylogenetic hypotheses depicted in this tree. Clade names are placed immediately below and to the left of their respective nodes, while branch support values are placed above and to the left. Negative values indicate that these groupings do not occur in the most parsimonious trees. Taxa abbreviations: AF, Artiofabula; CR, Cetruminantia; W, Whippomorpha.

wrist, an astragalar foramen, and a third trochanter on the femur (Thewissen et al., 1996).

Unlike the morphology-based matrix of O'Leary and Geisler (1999), the exclusion of Cetacea from Artiodactyla in all most parsimonious trees derived in this study is not entirely dependent on the inclusion of extinct taxa and their respective character codings in the phylogenetic analyses. If all extinct taxa and their characters codings are deleted from the morphological data set of this study, a parsimony analysis produces trees that have Cetacea excluded from the clade that includes living artiodactyls; however, Artiodactyla is not monophyletic in these trees because *Equus* forms the sister group to a ruminant and camel clade (fig. 10A). Even though Artiodactyla is not monophyletic in analyses with all data for extinct taxa excluded, the most parsimonious trees from the

analyses with all taxa (fig. 10B) are considerably shorter than the molecule-based trees of Gatesy et al. (1999b) (fig. 10C). Lengths of trees were calculated using the morphological matrix scored for extant taxa only. The shortest tree based on morphology that is also consistent with the most parsimonious trees from the analysis with all taxa is 610 steps long, while the shortest tree based on morphology that is consistent with the molecule-based hypothesis of Gatesy et al. (1999a) is 16 steps longer, or 626 steps. Even though the topology of the most parsimonious trees and the recovery of artiodactyl monophyly is sensitive to taxon sampling, morphological data contradict the molecule-based phylogeny with and without extinct taxa.

BASAL ARTIODACTYLS

Whereas there is general agreement on the monophyly of families within Artiodactyla, the higher level phylogeny within Artiodactyla is controversial, including which taxon occupies the most basal branch. *Diacodexis* has been suggested to be the most primitive artiodactyl by several authors (Matthew, 1934; Rose, 1985; Geisler and Luo, 1998; O'Leary and Geisler, 1999); however, both Rose (1982) and Gentry and Hooker (1988) hypothesized that *Diacodexis* is more closely related to selenodont artiodactyls based on structures in the limbs that they interpreted as cursorial adaptations. The most parsimonious trees for the morphology matrix of this study support a basal position for both species of *Diacodexis,* with Wasatchian *Diacodexis* being the sister group to a clade including *Diacodexis pakistanensis* and all other artiodactyls (figs. 8, 9). Placing both species of *Diacodexis* as sister groups to the clade of selenodont artiodactyls, which has *Bunomeryx* as its most basal member, increases tree length by 9 to 10 steps.

SUIFORM ARTIODACTYLS

There has been little consensus concerning the relationships of extinct artiodactyls to Hippopotamidae, Tayassuidae, and Suidae. In the analysis with some multistate characters ordered by O'Leary and Geisler (1999: fig. 8), *Elomeryx* and then *Archaeotherium*

(genus in artiodactyl family Entelodontidae) form successive sister groups to *Sus*. The placement of Entelodontidae as closer to Suina (Suidae + Tayassuidae) than to Hippopotamidae is also a feature of the preferred and most parsimonious trees of Gentry and Hooker (1988). In the morphology-based analyses of this study, Hippopotamidae and Suina (minus *Perchoerus*) form a clade to the exclusion of the extinct taxa Entelodontidae and *Elomeryx* (figs. 8, 9). This conclusion mirrors Matthew's (1929, 1934) early findings except for the more basal position of *Perchoerus*. A redefined Suiformes (see Introduction) is one of the more strongly supported, higher level, morphology-based clades within Artiodactyla, based on a branch support of three (fig. 8: taxon U), that contradicts recent molecule-based phylogenies (e.g., Gatesy et al., 1999b). Almost all of the characters that support Suoidea have been scored in one or more basal cetaceans; therefore, unlike characters of the hindlimb, these characters will continue to support an artiodactyl clade to the exclusion of Cetacea, regardless of future fossil discoveries.

Unlike the phylogenetic hypotheses of Gentry and Hooker (1988) and Colbert (1935), the results of this study indicate that anthracotheres (represented by *Elomeryx*) are not the sister group or potential ancestors to Hippopotamidae, but instead are the sister group to all other members of Suiformes (figs. 2, 3). A basal position for anthracotheres among suiform artiodactyls in this study corroborates similar views by Pickford (1983). Placing *Elomeryx* as the sister group to the Hippopotamidae causes an increase in 9 or 11 steps, depending on the position of this clade within Suiformes.

One surprising result of the phylogenetic analysis was a sister-group relationship between *Perchoerus,* which is considered a basal peccary, and a clade that includes extant members of Suina, Hippopotamidae, and Entelodontidae. Wright (1998: 391) listed the possession of a "Platelike posttympanic process of squamosal having rounded lateral edge" as a synapomorphy of Tayassuidae including *Perchoerus*. It is unclear exactly what this character refers to because this structure is rounded in *Sus* and *Tayassu*. In *Tayassu* and other peccaries, the posttympan-

ic process is expanded ventrally; however, the sutures between the tympanic and squamosal in available, juvenile specimens of *Perchoerus* are fused, making it impossible to determine if the squamosal is expanded. The teeth of *Perchoerus* resemble peccaries in lacking many of the cusps of pigs; however, the absence of these cusps is plesiomorphic for Artiodactyla. The enlarged, hypsodont upper and lower canines apparently ally *Perchoerus* with Suoidea; however, it is most parsimonious to place *Perchoerus* outside of this group based on several primitive characters, including absence of cancellous bone within the bulla, position of the foramen ovale anterior to or in line with the anterior edge of the glenoid fossa, and posterior edge of the foramen ovale formed by the alisphenoid. Trees that have a sister-group relationship between *Perchoerus* and *Tayassu* are eight steps longer than the most parsimonious trees. Entelodontidae plus extant suoids form a clade to the exclusion of *Perchoerus* in all most parsimonious trees. This group is supported by three unequivocal synapomorphies not found in *Perchoerus*: characters 16 (0 → 1), absence of contact between petrosal and basioccipital; 43 (1 → 0), posterolateral border of glenoid fossa flat; and 103 (0 → 1), M^2 and M^3 subequal.

SELENODONT ARTIODACTYLS

Controversial aspects of the phylogeny of selenodont artiodactyls include the affinities of Protoceratidae, monophyly of Neoselenodontia, monophyly of Tylopoda (sensu Webb and Taylor, 1980), and the affinities of Oreodontoidea. The taxonomic history of Protoceratidae is very complex, with previous workers advocating either ruminant or camelid affinities (see Patton and Taylor, 1973). According to several studies, Protoceratidae and Camelidae, to the exclusion of ruminants, comprise the two major groups within Tylopoda (Scott, 1940; Patton and Taylor, 1973; McKenna and Bell, 1997). By contrast, the most parsimonious trees for the matrix of Gentry and Hooker (1988) included a sister group relationship between Ruminantia and Protoceratidae; however, they rejected this hypothesis for a less parsimonious one that grouped Cameloidea and Protoceratidae

together. This study provides another alternative—that Protoceratidae (fig. 9: taxon T) is the sister group to a camel and ruminant clade. If Protoceratidae is placed as the sister group to Cameloidea (Camelidae + Oromerycidae), then the minimal length is 10 steps longer; if it is placed as the sister group to Cameloidea + *Cainotherium,* then the minimal length is 6 steps longer. Most of the characters listed by Patton and Taylor (1973) linking protoceratids with camels are primitive for artiodactyls (Janis et al., 1998), as determined here by optimization on the most parsimonious trees of this study and by comparison to *Diacodexis.* Examples include separation of the navicular and cuboid, magnum and trapezoid, and third and fourth metacarpals.

According to Webb and Taylor (1980), Tylopoda includes Camelidae, Oromerycidae, Xiphodontidae, Amphimerycidae, and Protoceratidae. As previously mentioned, this data matrix contradicts a close relationship between Protoceratidae and Camelidae. In all most parsimonious trees (figs. 8, 9), Ruminantia and Camelidae form a clade to the exclusion of Xiphodontoidea; therefore, tylopods form a paraphyletic group, with most tylopods being more distantly related to camels than ruminants are. Even though most tylopods do not appear to be closely related to camels, Cameloidea (Camelidae and Oromerycidae) occurs in all most parsimonious trees and corroborates the work of previous authors (Wortman, 1898; Scott, 1898, 1899, 1940) (fig. 9: taxon CA). Cameloidea is supported by the following synapomorphies in all most parsimonious trees: characters 64 (1 → 2), facial part of skull long; 65 (1 → 0), infraorbital canal over M^1 or P^4; 79 (1 → 0), depth of dentary constant between M_1 and M_3; 85 (1 → 0), lower canine larger than incisors; and 125 (0 → 1), anteroventral border of occipital condyle flared laterally. *Cainotherium* is the sister group to Cameloidea in the strict consensus, which is considerably different from the most parsimonious trees of Gentry and Hooker (1988), who placed Cainotheriidae as the sister group to a clade that includes all tylopods, Ruminantia, and Amphimerycidae. Based on this matrix, their phylogeny requires an additional 13 steps. Characters that support the grouping of *Cain-*

otherium with Camelidae and Oromerycidae are characters 28 (2 → 1), short meatal tube of the ectotympanic; 31 (0 → 1), posterior edge of squamosal sharply upturned; 43 (1 → 0), posterolateral edge of glenoid fossa flat and not notched; 45 (2 → 1), foramen ovale anterior to glenoid fossa or in line with its anterior edge; 57 (1 → 2), anterior edge of orbit over M^2 or M^2/M^3 division; 63 (0 → 1), anterior edge of jugal over M^1 or M^1/M^2 division; and 65 (2 → 1) facial infraorbital foramen over P^3/P^4 division.

Webb and Taylor (1980) named Neoselenodontia for the clade including tylopods and Ruminantia, and they listed characters to diagnose it. The most parsimonious trees for the matrix of Gentry and Hooker (1988) include a monophyletic Neoselenodontia; however, they discarded this hypothesis in favor of one that has a polyphyletic Neoselenodontia, with ruminants and camels evolving from two different groups of extinct artiodactyls. Stucky (1998) also favored a paraphyletic Neoselenodontia with *Homacodon* and *Bunomeryx* as basal members of a tylopod clade and the primitive artiodactyls *Pentacemylus* and *Mesomeryx* as the sister group(s) to Ruminantia. The phylogenetic analyses of the morphological matrix of this study support a monophyletic Neoselenodontia (figs. 8, 9: clade N); however, the support for this group is low, with branch support of one. Cameloidea, *Cainotherium,* and Ruminantia form a clade within Neoselenodontia to the exclusion of Xiphodontoidea and Protoceratidae in the strict consensus (fig. 8). The branch support for this clade is three, and it is supported by four unequivocal synapomorphies. Both Neoselenodontia and the clade excluding Xiphodontoidea and Protoceratidae contradict the molecule-based phylogeny of Gatesy et al. (1999a), which has Camelidae as the basal branch of Artiodactyla and Ruminantia as the sister group to Whippomorpha. Like one of the analyses of O'Leary and Geisler (1999: fig. 8), a sister-group relationship between Neoselenodontia and Oreodontoidea was also found in all most parsimonious trees. This position for Oreodontoidea contradicts Gentry and Hooker's (1988) conclusion that oreodonts are basal tylopods.

OTHER HYPOTHESES

Not only are the molecule-based clades Whippomorpha, Cetruminantia, and Artiofabula not in any of the most parsimonious trees of this study, they are strongly contradicted by the morphological data in appendix 3. Trees consistent with the molecule-based hypothesis of Gatesy et al. (1999a) are at least 25 steps longer than the most parsimonious trees. A substantial amount of the data presented in this study has not been previously included in a cladistic analysis; therefore, these tests are novel. As with molecular data (Gatesy et al., 1999b), the addition of new morphological data corroborates previous morphology-based hypotheses and does not lead to novel phylogenetic hypotheses. The most parsimonious trees for appendix 3 include most of the clades found by O'Leary and Geisler (1999: fig. 8), such as Artiodactyla, Suiformes, Neoselenodontia, and a clade including Mesonychidae + Hapalodectidae + Cetacea.

Despite the rejection of molecule-based hypotheses by this study, the strict consensus in figure 8 should not be taken as the best, overall hypothesis for artiodactyl and cetacean phylogeny. Both molecular and morphological data can test phylogenetic hypotheses as well as be explained by them; therefore, the best hypothesis should be based on a combined analysis of both types of data (Nixon and Carpenter, 1996). A project in progress aims to do just that (Geisler, in prep.); however, a caveat of such "total evidence" projects is that characters interpreted as homoplasy remain unexplained. Until an alternative explanation is presented, the phylogeny in figure 8 is the *best* explanation for morphological data and *potentially* falsifies the molecule-based hypotheses. The challenge for future studies is to develop hypotheses that simultaneously explain conflicting types of data. Such attempts will certainly require us to go beyond the boundaries of a most parsimonious cladogram for a scientific explanation.

ACKNOWLEDGMENTS

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APPENDIX 1

SPECIMENS AND REFERENCES

Two of the OTUs were families, and the allocation of genera to Leptictidae and Entelodontidae follows McKenna and Bell (1997).

OUTGROUPS

Ictops: AMNH-VP 38920, 76745.
Leptictis: AMNH-VP 1413a, 5346, 38920, 39444, 90256, 96766; MCZ 19678; USNM 336367; Matthew (1918); Novacek (1980, 1986).
Orycteropus afer: AMNH-VP 2285.

OTHER NONUNGULATE MAMMALS

Vulpavus: AMNH-VP 1900, 19198, 11497, 12626; Heinrich and Rose (1997).
Canis: AMNH-VP 2288, 2853, 3043; Evans (1993).
Rattus norvegicus: AMNH-VP 180, 181, 2925; Greene (1935).

ARCHAIC UNGULATES

Arctocyon: AMNH-VP 55900 (cast), 55901 (cast), 55902; Russell (1964).
Eoconodon: AMNH-VP 764, 774, 3177, 3181, 3187, 3280, 4052, 16329, 16341; Matthew (1897, 1937).
Hyopsodus: AMNH-VP 1, 39, 1717, 10977, 10979, 11330, 11349, 11350, 11363, 11393, 11415, 11899; Gazin (1968); Thewissen and Domning (1992).
Meniscotherium: AMNH-VP 2560, 4412, 4413, 4414, 4426, 4434, 4447, 48083, 48120, 48121, 48122, 48125, 48126, 48127, 48129, 48555; Gazin (1965); Cifelli (1982); Williamson and Lucas (1992).
Phenacodus: AMNH-VP 293, 2961 (cast), 4370, 4378, 4403, 15262, 15266, 15268, 15271, 15275, 15279, 15286, 16791, 16794, 117195 (cast); Thewissen (1990).

CETACEA

Ambulocetus natans: HGSP 18507; Thewissen et al. (1996).

Balaenoptera: AMNH-M 28274, 84870, 148407, 219212, 219220; Daudt (1898); Müller (1898); Sokolov (1982).

Basilosaurus: AMNH-VP 141381, 61990, 129577; GSP-UM 97507 (cast); Kellogg (1936).

Delphinapterus leucas: AMNH-M 34868, 34937, 34944, 77789, 185300.

Georgiacetus vogtlensis: GSM 350; Hulbert et al. (1998); Hulbert (1998).

Pakicetus: GSP-UM 084 (cast), HGSP 96231, 96386, 96431; Gingerich and Russell (1981, 1990); Thewissen and Hussain (1993); Thewissen (1994); Luo (1998).

Physeter catodon: AMNH-M 80206, 34872; Omura et al. (1962).

Protocetus atavus: SMNS 11084, Fraas (1904).

Remingtonocetus harudiensis: GSP-UM 3009, 3054, 3057; Kumar and Sahni (1986); Gingerich et al. (1995).

Tursiops truncatus: AMNH-M 120920, 184930, 212554; Slijper (1966); Fanning and Harrison (1974).

MESONYCHIDAE

Dissacus navajovius: AMNH-VP 3356, 3359, 3360, 3361, 15996.

Dissacus praenuntius: AMNH-VP 16069, 131919 (cast); O'Leary and Rose (1995a); Luo and Gingerich (1999).

Mongolian *Dissacus*: MAE-BU97–13786.

Harpagolestes: AMNH-VP 1692, 1878, 1892, 1945, 2302, 2308, 26267, 26300, 26301; Wortman (1901); Zhou et al. (1995).

Mesonyx obtusidens: AMNH-VP 11552, 12643, 93451; Scott (1888).

Pachyaena gigantea: AMNH-VP 72, 2959, 15226, 15227; O'Leary and Rose (1995b); Rose and O'Leary (1995).

Pachyaena ossifraga: AMNH-VP 75, 4262, 4263, 15222, 15224, 15730, 16154; O'Leary and Rose (1995b).

Sinonyx jiashanensis: IVPP V10760; Zhou et al. (1995).

Synoplotherium canius: AMNH-VP 19203; Wortman (1901).

HAPALODECTIDAE

Hapalodectes hetangensis: IVPP V5253; Ting and Li (1987).

Hapalodectes leptognathus: AMNH-VP 78, 12781, 128561, 14748 (cast); Szalay (1969); O'Leary (1998b).

ARTIODACTYLA

Agriochoerus: AMNH-VP 685, 1349, 1178, 1355, 1490, 7402, 7406, 7407, 7409, 7410, 7420, 9808, 9811, 38843, 38932, 95324, 95332, 99275.

Amphimeryx: Stehlin (1910); Pearson (1927); Dechaseaux (1974).

Archaeotherium: AMNH-VP 569, 1277, 1278, 1483, 2176, 6389, 7380, 11323, 12461, 26176, 39010, 39018, 39127, 39455, 53602, 53609, 82454, 90101, 102091, 18–537.

Bos taurus: AMNH-M 147192, 147193, 147194, 180379, 212982, 212986, 212987; Sisson (1921); Dyce et al. (1987).

Bunomeryx montanus: AMNH-VP 2066, 2070, 2071; Norris (1999).

Cainotherium: AMNH-VP 10277, 55333, 55337; Hürzeler (1936).

Camelus: AMNH-M 2911, 14109, 35379, 35463, 35563, 63850, 69405, 80227, 90433; Smuts and Bezuidenhout (1987).

Cebochoerus: AMNH-VP 111093, 11094, 11095, 105081, 105458; Pearson (1927); Dechaseaux (1974).

Diacodexis pakistanensis: Russell et al. (1983); Thewissen et al. (1983); Thewissen and Hussain (1990).

Wasatchian *Diacodexis* (probably *D. metsiacus*): AMNH-VP 4700, 16141, 128563 (cast); Rose (1985).

Elomeryx armatus: AMNH-VP 572, 579, 582, 1242, 1243, 1245, 1249, 1259, 1263, 1483, 39015, 10041, 12461, SD 582, SD 23–491, 511, 101668; Scott (1894).

Entelodon: AMNH-VP 7380.

Eotylopus reedi: AMNH-VP 53.4 (cast), 784, 47394, 47404, 88301; Scott (1940).

Gobiohyus orientalis: AMNH-VP 26277, 26274, 26282.

Heteromeryx dispar: AMNH-VP 12326.

Hexaprotodon liberiensis: AMNH-M 2423, 52465, 81899, 89626, 146848, 146849, 148452, 185383, 202423, 214182; Sokolov (1982).

Hippopotamus amphibius: AMNH-M 130247, 15898, 176118, 24282, 24284, 24287, 24285, 24289, 53773, 54248, 54249, 80183, 80813, 81856, 99637, 130247, 70019; Langer (1988); Sokolov (1982).

Homacodon vagans: AMNH-VP 12695, 12138, 12139; Marsh (1894).

Hypertragulus: AMNH-VP 53802, 1341, 53804, 7918, 53801, 53803, 7944, 7933, Lusk-0-146-4024, (H) 326–654.

Lama: AMNH-M 14121, 146543, 70424, 6291, 6235, 40842, 100276, 247748, 46, 40846, 147879, 80113.

Leptomeryx: AMNH-VP 53710, 53721, 11870,

38910, 53663, 39123, 53711, 6616, 39450, 53571, (S) 606–25834, 542–24617, 611–26621.

Leptoreodon marshi: AMNH-VP 2064.

Merycoidodon: AMNH-VP 1287, 39425, 45250; FAM 49690, 72205, 72238, 72258, 45217A, 45217B, 72186B, 49644, 72286; AM 595, 1297, 610, 9793, 594.

Mixtotherium: AMNH-VP 10443, 10445, 100019, 107617, 105080; Stehlin (1908); Pearson (1927); Dechaseaux (1974).

Odocoileus virginianus: AMNH-M 152, 7377, 24410, 37617, 20797, 244603, 238469, 238644, 245629, 238469.

Ovis: AMNH-M 875, 6231, 6239, 35520, 88702, 10074, 10261, 14515, 15584, 35316, 35816, 35851, 70084, 80120, 100072, 119634, 146547, 53589; Sokolov (1982).

Perchoerus: AMNH-VP 585, 695, 1200, 1282, 1285, 7391, 7392, 7394, 7395, 7398, 9794, 9813.

Poebrotherium: AMNH-VP 6515, 8955, 9352, 9804, 13034, 38990, 39085, 39446, 41317, 42240, 42248, 42249, 42261, 42272, 42276, 42277, 42281, 42284, 42290, 42292, 47003, 47008, 47016, 47022, 47027, 47052, 47093, 47103, 47182, 47284, 47317, 47324, 47333, 47707A, 47707B, 47907, 63704, 63712, 63713, 63756, 63757, 63761, 97103.

Protoceras celer: AMNH-VP 1228, 584, 1222, 1223, 1224, 1220, 1229, 53521, 1226, 53527, 1227, 644, 40878, 40879, 597, 643.

Sus scrofa: AMNH-M 45, 5450, 20871, 54508, 69422, 100260, 135020, 235190, 235192, 236144, 236145, 238325, 238331, 694422; Sokolov (1982).

Tayassu tajacu: AMNH-M 66748, 25978, 28954, 28955, 36703, 29446, 29442, 141992, 215154, 17352.

Tragulus: AMNH-M 548, 32645, 37210, 53602, 53609, 60759, 90101, 90193, 10101, 102091, 102176, 103700, 14137, 14139, 34252, 106552, 188310, 240913, 244375.

Xiphodon: Cuvier (1822); Stehlin (1910); Dechaseaux (1967).

PERISSODACTYLA

Equus caballus: AMNH-VP 272, 273, FM 99, FM 129; Sisson (1921); Langer (1988).

Mesohippus: AMNH-VP 673, 74001, 74019, 74025, 74048, 74063, 111744, 116325, 116344, 116345, 116374.

Heptodon: AMNH-VP 294, 485, 4858, 14884, 16861, 141881, 14864, 14865, 16861; Radinsky (1965).

Hyracotherium: AMNH-VP 118, 55267, 55268, 55269, 70197, 96274, 96277, 96283, 96298, 96734, 129209; Thewissen and Domning (1992).

APPENDIX 2

MORPHOLOGICAL CHARACTERS

This appendix defines the 176 morphological characters used for cladistic analyses. Unqualified citations indicate that the character is worded with little or no modification from the given reference. Characters that are "modified" from references have been significantly changed, and those that are "derived" have been extracted from a diagnosis or morphological description and converted into a form ready for cladistic analysis. Multiple citations indicate more detailed descriptions, additional character states, illustrations, or other improvements of a character, as compared to its first use.

VASCULAR

1. *Medial edge of ectotympanic bulla.*—Not notched (0); has notch and sulcus for the internal carotid artery (1) (modified from Webb and Taylor, 1980).
2. *Transpromontorial sulcus for the internal carotid artery.*—Present, forms antero-posterior groove on promontorium, medial to the fenestrae rotundum and ovalis (0); absent (1) (Cifelli, 1982; Thewissen and Domning, 1992).
3. *Internal carotid foramen.*—Absent or confluent with piriform fenestra (0); present at basisphenoid/basioccipital suture with lateral wall of foramen formed by both these bones and thus separated from the piriform fenestra (1) (Geisler and Luo, 1998).
4. *Sulcus on promontorium for proximal stapedial artery.*—Present, forms a groove that branches from the transpromontorial sulcus anteromedial to the fenestra rotundum and extends to the medial edge of the fenestra ovalis (0); absent (1) (Cifelli, 1982; Thewissen and Domning, 1992).
5. *Foramen for ramus superior of stapedial artery.*—Present (0); absent (1) (modified from Novacek, 1986; Thewissen and Domning, 1992).
6. *Position of foramen for ramus superior of stapedial artery.*—Lateral to epitympanic

recess (0); anterolateral to epitympanic recess, adjacent to ventrally convex portion of the tegmen tympani (1). Cannot be scored for taxa that lack this foramen (modified from Geisler and Luo, 1998; O'Leary and Geisler, 1999).

7. *Size of postglenoid foramen.*—Large, much larger than fenestra ovalis of petrosal (0); small, slightly larger than or equal in size to the fenestra ovalis; absent (1) (modified from Geisler and Luo, 1998; O'Leary and Geisler, 1999)

8. *Position of postglenoid foramen* (ordered).—Enclosed entirely by the squamosal (0); situated on petrosal/squamosal suture, and if bulla present, a secondary ventral opening between the bulla and the squamosal may form (1) (modified from Geisler and Luo, 1998; O'Leary and Geisler, 1999).

9. *Mastoid foramen.*—Present, skull in posterior view (0); absent (1) (see MacPhee, 1994).

10. *Posttemporal canal (for arteria diploetica magna, also called percranial foramen).*—Present, occurs at petrosal/squamosal suture with skull in posterior view, the canal continues within the petrosal/squamosal suture (0); absent (1) (Wible, 1990; MacPhee, 1994).

OTIC REGION AND SURROUNDING FEATURES

11. *Subarcuate fossa.*—Present (0); absent (1) (Novacek, 1986).

12. *Shape of tegmen tympani* (ordered).—Uninflated, forms lamina lateral to facial nerve canal (0); inflated, forms barrel-shaped ossification lateral to the facial nerve canal (1); hyperinflated, transverse width of tegmen tympani greater than or equal to width of promontorium (2) (modified from Cifelli, 1982; Geisler and Luo, 1998; Luo and Gingerich, 1999; O'Leary and Geisler, 1999).

13. *Anterior process of petrosal.*—Absent (0); present, anterior edge of tegmen tympani far anterior to edge of promontorium (1) (Geisler and Luo, 1998; Luo and Gingerich, 1999).

14. *Fossa for tensor tympani muscle.*—Shallow anteroposteriorly elongate fossa (0); circular pit, no groove (1); circular pit with deep tubular anterior groove (2); long narrow groove between tegmen tympani and promontorium (3) (Geisler and Luo, 1998; Luo and Gingerich, 1999).

15. *Stylomastoid foramen.*—Incomplete, ectotympanic contacts tympanohyoid laterally and petrosal medially, in some cases ectotympanic separated from petrosal by a narrow fissure (0); complete, ectotympanic contacts both the tympanohyoid and the petrosal (1) (modified from Geisler and Luo, 1998; O'Leary and Geisler, 1999; Luo and Gingerich, 1999).

16. *Articulation of pars cochlearis with basisphenoid/basioccipital.*—Present (0); absent (1) (Thewissen and Domning, 1992).

17. *Ectotympanic.*—Simple ring (0); medial edge expanded into bulla (1). Cannot be scored for taxa in which the ectotympanic is not preserved (derived from Novacek, 1977; MacPhee, 1981).

18. *Ectotympanic bulla.*—Thin-walled, contains middle ear space only (0); houses middle ear space and highly cancellous bone (1) (Gentry and Hooker, 1988).

19. *Pachyosteosclerotic involucrum of bulla.*—Absent (0); present (1) (Thewissen, 1994; Luo, 1998).

20. *Lateral furrow of tympanic bulla.*—Absent (0); present, forms a groove on the lateral surface of the ectotympanic bulla anterior to the base of the sigmoid process (1) (Geisler and Luo, 1998; Luo and Gingerich, 1999).

21. *Ventral inflation of ectotympanic bulla* (ordered).—Absent, ventral edge of bulla dorsal to ventral edge of occipital condyles (0); intermediate, edge of bulla at same level as occipital condyles (1); present, ventral edge of bulla ventral to occipital condyles (2).

22. *Posterior extension of bulla.*—Absent, stylohyoid does not rest in notch on posterior edge of bulla (0); present, bulla expanded around stylohyoid forming notch on posterior edge of bulla (1); bulla extends posterior to stylohyoid medially (2); bulla extends posterior to stylohyoid laterally (3); dorsal end of stylohyoid completely enveloped or nearly so by bulla (4) (modified from Gentry and Hooker, 1988).

23. *Orientation of stylohyoid.*—Ventral or ventrolateral, may rest in notch on the posterior edge of a tympanic bulla (0); anteroventral, may rest in longitudinal furrow on ventral surface of a tympanic bulla (1).

24. *Articulation of ectotympanic bulla to squamosal* (ordered).—Broad articulation with medial base of postglenoid process (0); circular facet on elevated stage (1);

contact reduced to the falcate process of the squamosal (2); contact absent (3) (Geisler and Luo, 1998; Luo and Gingerich, 1999).

25. *Contact between exoccipital and ectotympanic bulla.*—Absent (0), present (1) (Geisler and Luo, 1998; Luo and Gingerich, 1999).

26. *Sigmoid process (homologous to anterior crus of tympanic ring).*—Absent (0); present, forms transverse plate that projects dorsolaterally from the anterior crus of the ectotympanic ring and forms the anterior wall of the external auditory meatus (1) (modified from Thewissen, 1994; Geisler and Luo, 1998; Luo and Gingerich, 1999).

27. *Morphology of sigmoid process.*—Thin and transverse plate (0); broad and flaring, base of the sigmoid process forms dorsoventral ridge on lateral surface of ectotympanic bulla (1) (Geisler and Luo, 1998; Luo and Gingerich, 1999).

28. *Ectotympanic part of the meatal tube* (ordered).—Absent (0); present but short, length of tube <30% the maximum width of the bulla (1); present and long, length >60% maximum width of bulla (2) (Geisler and Luo, 1998).

29. *Basioccipital crests (falcate processes).*—Absent (0); present, form ventrolaterally flaring basioccipital processes (1) (derived from Barnes, 1984; modified from Thewissen, 1994; Geisler and Luo, 1998).

GLENOID, POSTGLENOID, AND TEMPORAL REGIONS

30. *Paroccipital process* (ordered).—Short, in posterior view distal end terminates dorsal to ventral edge of occipital condyle (0); intermediate size, extends just ventral to ventral edge of condyle (1); elongate, terminates far ventral to occipital condyle (2).

31. *Posterior edge of squamosal.*—Flat (0); sharply upturned (1); sharply upturned and bears dorsally projecting process (2) (modified from Gentry and Hooker, 1988).

32. *Lambdoidal crest.*—Present (0); absent or forms low ridge (1).

33. *Sagittal crest* (ordered).—Absent or barely present, dorsoventral thickness of crest <7% of dorsoventral height of braincase (measured from ventral edges of condyles to dorsalmost point of supraoccipital) (0); small, 10%< sagittal crest thickness

<15% of braincase height (1); substantial, 20%< sagittal crest thickness <33% of braincase height (2); dorsally expanded, 39%< sagittal crest thickness <52% of braincase height (3).

34. *Dorsal edge of braincase, relative to occlusal plane.*—Slopes posterodorsally (0); approximately level relative to upper toothrow (1); curves posteroventrally (2).

35. *Facial nerve sulcus distal to stylomastoid foramen.*—Absent (0); anterior wall of sulcus formed by squamosal (1); anterior wall formed by mastoid process of petrosal (2); anterior wall formed by meatal tube of ectotympanic (3) (modified from Geisler and Luo, 1998; O'Leary and Geisler, 1999).

36. *Length of mastoid process of petrosal* (ordered).—Ventral portion absent (0); ventral portion short, <70% of the anteroposterior length of promontorium (1); elongate, >100% length of promontorium (2); hypertrophied, >200% length of promontorium (3) (modified from Geisler and Luo, 1996; Luo and Marsh, 1996; Geisler and Luo, 1998).

37. *Lateral exposure of mastoid process of petrosal* (ordered).—Present between exoccipital and squamosal (0); constricted, dorsal part of exposure forms lamina (1); absent (2) (modified from Geisler and Luo, 1996; Luo and Marsh, 1996).

38. *Mastoid process of petrosal.*—Exposed externally on posterior face of braincase as a triangle between the lambdoidal crest of the squamosal dorsolaterally, the exoccipital ventrally, and the supraoccipital medially (0); not exposed posteriorly, lambdoidal crest of squamosal in continuous contact with exoccipital and supraoccipital (1).

39. *Angle of suture of squamosal with petrosal or exoccipital, skull in ventral view* (ordered).—Very large, forms a 147° angle with the sagittal plane (0); large, forms an angle between 127° and 125° (1); angle between 111° and 105° (2), angle <100° (3).

40. *Length of external auditory meatus of the squamosal* (ordered).—Very short or absent, length <4% of half the basicranial width (0); short, length between 19% and 23% (1); intermediate length between 29% and 36% (2); long, length between 41% and 45% (3); very long, length >52%.

41. *Postglenoid process.*—Forms transversely oriented and ventrally projecting ridge

(0); ventrally projecting prong, roughly oval in coronal section (1).

42. *Glenoid fossa.*—Concave longitudinally (0); flat longitudinally (1); convex longitudinally (2).

43. *Posterolateral border of glenoid fossa.*— Slightly downturned ventrally or flat (0); conspicuously notched with concave surface facing posteroventrally (1).

44. *Preglenoid process.*—Absent (0); present, forms transverse, ventrally projecting ridge at anterior edge of glenoid fossa (1) (modified from Thewissen, 1994; Geisler and Luo, 1998).

45. *Foramen ovale.*—Anterior to glenoid fossa (0); medial to glenoid fossa (1) (derived from Zhou et al., 1995; Geisler and Luo, 1998).

46. *Posterior edge of foramen ovale.*— Formed by the alisphenoid (0); formed by the petrosal and or tympanic bulla (1); formed by squamosal (2).

47. *Dorsoventral thickness of zygomatic process of the squamosal* (ordered).—Small, 7%< dorsoventral thickness of zygomatic process <15% of dorsoventral height of braincase (measured from ventral edges of condyles to dorsalmost point of supraoccipital) (0); intermediate, 17%< dorsoventral thickness of zygomatic process <28% of dorsoventral height of braincase (1); dorsoventrally deep, 32%< dorsoventral thickness of zygomatic process <40% of dorsoventral height of braincase (2).

48. *Zygomatic portion of jugal.*—Directed posterolaterally (0); directed posteriorly (1).

ORBITAL MOSAIC AND FORAMINA

49. *Alisphenoid canal (alar canal).*—Present (0); absent (1) (Novacek, 1986; Thewissen and Domning, 1992).

50. *Foramen rotundum.*—Absent, maxillary division of trigeminal nerve exits skull through the sphenorbital fissure (0); present (1) (Novacek, 1986; Thewissen and Domning, 1992).

51. *Contact of frontal and alisphenoid.*—Present (0); absent, separated by orbitosphenoid (1) (Prothero, 1993).

52. *Contact of frontal and maxilla in orbit.*— Absent (0); present (1) (Novacek, 1986; Thewissen and Domning, 1992).

ORBITAL POSITION AND SURROUNDING FEATURES

53. *Supraorbital horns.*—Absent (0); present,

unbranched (1); present, branched (2) (Janis and Scott, 1987; Scott and Janis, 1993).

54. *Supraorbital process.*—Absent, region over orbit does not project lateral from sagittal plane (0); present, laterally elongate and tabular (1) (derived from Barnes, 1984; Geisler and Luo, 1998).

55. *Postorbital process of jugal* (ordered).— Absent (0); present but does contact frontal (1); present and contacts postorbital process of frontal forming postorbital bar (2) (modified from Gentry and Hooker, 1988).

56. *Ventral edge of orbit.*—Projects dorsally (0); flared laterally (1).

57. *Position of orbit relative to toothrow* (ordered).—Over P^4 or P^4/M^1 division (0); over M^1 or M^1/M^2 division (1); over M^2 or M^2/M^3 division (2); over or posterior to M^3 (3).

58. *Lacrimal tubercle.*—Absent (0); present, situated on anterior edge of orbit adjacent to the lacrimal foramen (1) (Novacek, 1986).

59. *Lacrimal foramina* (ordered).—Two (0); one (1); highly reduced (2); absent (3) (modified from Gentry and Hooker, 1988).

60. *Facial portion of lacrimal relative to the orbit* (ordered).—Restricted to orbital rim, 15%< maximum anteroposterior length of facial portion of lacrimal <30% of the maximum anteroposterior diameter of the orbit (0); small facial portion present, 30%< length of facial portion of lacrimal <67% of the orbital diameter (1); moderate facial portion present, 70%< length of facial portion of lacrimal <93% of the orbital diameter (2); large facial portion present, 100%< length of facial portion of lacrimal <180% of the orbital diameter (3).

61. *Antorbital pit in lacrimal.*—Absent (0); present (1) (Janis and Scott, 1987; Scott and Janis, 1993).

62. *Fenestra in rostrum at junction of lacrimal, nasal, and maxilla.*—Absent (0); present (1) (Scott and Janis, 1993).

63. *Position of anterior edge of jugal* (ordered).—Anterior to or over P^4 (0); over M^1 or M^1/M^2 division (1); over M^2 or M^2/M^3 division (2); over or posterior to M^3 (3).

FACE AND PALATE

64. *Elongation of face* (ordered).—Absent

and face short, face (defined as part of skull anterior to anterior edge of orbit) <85% of the remaining posterior part of the skull (defined as part between anterior edge of orbit and posterior edge of occipital condyle) (0); long, 90% < face < 170% remaining part of skull (1); elongate, 190% < face < 230% remaining part of skull (2).

65. *Anterior opening of infraorbital canal* (ordered).—Over M^1 or P^4 (0); at level between P^3 and P^4 (1); anterior or over P^3 (2).

66. *Lateral surface of maxilla.*—Flat or slightly concave (0); highly concave (1).

67. *Posterior edge of nasals.*—Terminate anterior to orbit (0); extended posteriorly, terminate posterior to the anterior edge of the orbit (1).

68. *Palatine fissures* (ordered).—Enlarged, transverse distance between lateral edges of palatine fissures >53% of the width of the palate in the same transverse plane (0); small, transverse distance between lateral edges of palatine fissures <48% of the width of the palate in the same transverse plane (1); absent (2).

69. *Palate.*—Flat (0); vaulted, portion along sagittal plane well dorsal to lateral edge (1).

70. *Embrasure pits on palate.*—Absent (0); present, situated medial to the toothrow, accommodate the cusps of the lower dentition when the mouth is closed (1) (modified from Thewissen, 1994; Geisler and Luo, 1998).

71. *Posterior margin of external nares* (ordered).—Anterior to or over the canines (0); between P^1 and P^2 (1); posterior to P^2 (2) (Geisler and Luo, 1998).

MANDIBULAR

72. *Angular process of mandible.*—No dorsal hook (0); dorsal hook present (1) (Gentry and Hooker, 1988).

73. *Angle of mandible.*—Distal end at same level as ventral edge of dentary below molars (0); forms distinct flange that projects posteroventrally well below ventral edge of dentary below molars (1) (modified from Gentry and Hooker, 1988).

74. *Mandibular foramen* (ordered).—Small, maximum height of opening 25% or less the height of the mandible at M_3 (0); enlarged and continuous with a large posterior fossa, maximum height greater than 50% the height of the mandible at M_3 (1)

(modified from Thewissen, 1994; Geisler and Luo, 1998).

75. *Elongation of coronoid process* (ordered).—Absent, 50%< dorsal height of coronoid process <90% of the width of the coronoid process (measurement taken at posterior base of coronoid process, immediately anterior to mandibular condyle) (1); moderate, 110%< dorsal height <180% of its width (2); substantial, 200%< dorsal height <270% of its width (3).

76. *Height of coronoid process* (ordered).—Low, 150%< height of coronoid (measured from ventral edge of mandible to dorsal edge of coronoid) <190% of the depth of the mandible at M_3 (0); high, 210%< height of coronoid <310% of the depth of the mandible at M_3 (1); very high, 320%< height of coronoid <440% of the depth of the mandible at M_3 (2).

77. *Deep concavity on lateral surface of mandible between condyle and coronoid process of dentary.*—Absent (0); present (1) (modified from Gentry and Hooker, 1988).

78. *Height of dentary condyle* (ordered).—Low, 60%< height of condyle (measured from ventral edge of mandible to dorsal edge of condyle but excluding any portion of the mandible that extends ventrally below the edge of the mandible at M_3) <140% of the depth of the mandible at M_3 (0); moderately elevated, 160%< height of condyle <230% of the depth of the mandible (1); well elevated, 240%< height of condyle <300% of the depth of the mandible (2).

79. *Ramus of mandible.*—Approximately same dorsoventral thickness from M_1 to M_3 (0); deepens posteriorly from M_1 to M_3 (1) (modified from Gentry and Hooker, 1988).

80. *Mandibular symphysis.*—Unfused (0); fused (1) (Pickford, 1983).

INCISORS AND CANINES

81. I^1 *and* I^2.—Present (0); absent (1).

82. *Rostrum.*—Premaxillae short with incisors arranged in transverse arc (0); premaxillae elongate, incisors aligned longitudinally with intervening diastemata (1) (modified from Prothero et al., 1988; Thewissen, 1994).

83. *Lower incisors.*—Apex of cusp pointed or narrower than base (0); spatulate, apex of cusp wider than base (1); peg-shaped,

width of base equal to width of tip of tooth (2); tusklike (3).

84. *Elongation and transverse compression of upper canines.*—Absent (0); present (1). If sexually dimorphic, score for males only (modified from Webb and Taylor, 1980).

85. *Lower canine size.*—Larger than incisors (0); approximately same size as incisors (1).

86. *Lower canine shape.*—Oval in cross section (0); triangular or D-shaped and pointing anteriorly (if D-shaped, rounded portion directed anteriorly) (1) (modified from Gentry and Hooker, 1988).

87. *Lower canine.*—Consists of a distinct crown and root (0); hypsodont, no clear boundary between crown and root (1) (Pickford, 1983).

PREMOLARS

88. *P^1* (ordered).—Absent (0); present, one-rooted (1); present, two-rooted (2) (Zhou et al., 1995; O'Leary, 1998a).

89. *P_1.*—Present (0); absent (1) (Zhou et al., 1995).

90. *P_1 morphology.*—Low, transversely compressed cusp (0); caniniform, single cusp high and pointed (1); molariform, two main cusps in trigonid followed by compressed talonid basin (2) (modified from Gentry and Hooker, 1988).

91. *P^3 roots.*—Three (0); two (1) (Zhou et al., 1995).

92. *P_3 metaconid.*—Absent (0); present (1) (Thewissen and Domning, 1992).

93. *P^4 protocone.*—Present (0); absent (1) (Thewissen, 1994).

94. *P^4 paracone.*—Equal or subequal to height of paracone of M^1 (0); greater than twice the height of M^1 paracone (1) (Thewissen, 1994).

95. *P^4 metacone.*—Absent (0); present (1).

96. *P^4 entocingulum.*—Present, partially or completely surrounds the base of protocone (0); absent or very small (1).

97. *P_4 metaconid.*—Absent (0); present (1) (Thewissen and Domning, 1992).

98. *Deciduous P_4.*—Resembles M_1 (0); six-cusped with additional neomorphic cusp on paracristid (1) (derived from Gentry and Hooker, 1988; Luckett and Hong, 1998).

MOLARS

99. *M^1 parastyle* (ordered).—Absent (0);

weak (1); moderate to strong (2) (Zhou et al., 1995; O'Leary, 1998a).

100. *M_1 metaconid.*—Present (0); absent (1) (Thewissen, 1994).

101. *M^2 metacone* (ordered).—Distinct cusp, subequal to paracone (0); distinct cusp, approximately half the size of the paracone (1); highly reduced, indistinct from paracone (2) (Zhou et al., 1995; O'Leary, 1998a).

102. *M_2 metaconid.*—Present, forms distinct cusp (0); absent or occasionally present as swelling on lingual side of protoconid (1) (modified from Zhou et al., 1995).

103. *M^3* (ordered).—Present, larger than M^2 (0); present, approximately equal (1); reduced, maximum mesodistal length <60% the length of M^2 (2); absent (3) (modified from Zhou et al., 1995; Geisler and Luo, 1998).

104. *M_3 metaconid.*—Present, forms distinct cusp (0); absent or occasionally present as swelling on lingual side of protoconid (1). Cannot be scored for taxa that lack M_3 (modified from Zhou et al., 1995).

105. *M_3 hypoconulid* (ordered).—Long, protrudes as separate distal lobe (0); reduced, does not protrude substantially beyond rest of talonid (1); absent (2) (Thewissen, 1994).

106. *Parastyle or preparacrista position.*—Lingual position, in line with or lingual to a line that connects the paracone or metacone (0); labial position, labial to the line that connects the paracone and metacone.

107. *Molars.*—Have stylar shelves (0); stylar shelves absent (1).

108. *Ectocingula on upper molars.*—Present (0); absent (1) (O'Leary, 1998a).

109. *Mesostyle on upper molars.*—Absent (0); present but much lower than paracone and metacone (1); present and high with crests connecting to paracone and metacone (2).

110. *Paraconule of upper molars* (ordered).—Present (0); reduced (1); absent (2) (O'Leary, 1998a).

111. *Number of cusps in posterolingual quadrant of M^1 and M^2* (ordered).—Two, both hypocone and metaconule present (0); one, hypocone or metaconule present (1); none, both hypocone and metaconule absent (2).

112. *Protoloph.*—Absent (0); present (1) (Hooker, 1989).

113. *Metaloph.*—Absent (0); present (1) (Hooker, 1989).

114. *Lingual cingulid on molars.*—Poorly de-

fined or absent (0); continuous to mesial to distal extreme (1) (O'Leary, 1998a).

115. *Lower molar paraconid or paracristid position.*—Cusp lingual or crest winds lingually (0); cusp anterior or crest straight mesodistally on lingual margin (1) (O'Leary, 1998a).

116. M_1 *and* M_2 *hypoconulid.*—Absent (0); present (1) (Gentry and Hooker, 1988).

117. *Crest connecting entoconid and hypoconid to the exclusion of the hypoconulid on lower molars (hypolophid).*—Absent (0); present (1) (Gentry and Hooker, 1988).

118. *Metastylid of lower molars.*—Absent (0); present (1) (Gentry and Hooker, 1988).

119. *Entoconulid of lower molars.*—Absent (0); present (1) (Gentry and Hooker, 1988).

120. *Molar protoconid.*—Subequal to height of talonid (0); closer to twice height of talonid or greater (1) (O'Leary, 1998a).

121. *Loph formation on anterior aspect of lower teeth.*—Absent (0); present (1) (Hooker, 1989).

122. *Reentrant grooves* (ordered).—Proximal (0); absent (1); distal (2) (Thewissen, 1994; O'Leary, 1998a).

123. *Talonid basins.*—Broad, hypoconid and entoconid present (0); compressed, with hypoconid displaced lingually and centered on the width of the tooth, entoconid absent (1) (modified from Zhou et al., 1995; description based on O'Leary and Rose, 1995a; Geisler and Luo, 1998).

OCCIPITAL CONDYLES AND VERTEBRAL

124. *Occipital condyles.*—Broadly rounded in lateral view (0); V-shaped in lateral view, in posterior view the condyle is divided into a dorsal and a ventral half by a transverse ridge (1).

125. *Anteroventral border of occipital condyle.*—Tapers medially (0); flared laterally and ventrally to form stop for ventral movement of the cranium (1).

126. *Odontoid process of axis.*—Forms anteriorly pointed peg (0); spoutlike, dorsal surface forms concave trough (1); bears central dorsal ridge that separates two spoutlike troughs (2) (modified from Webb and Taylor, 1980).

127. *Atlantoid facet of axis vertebra.*—Restricted below neural arch or extends slightly dorsal to the base of the neural pedicle (0); extended dorsally at least halfway up neural arch (1) (modified from Webb and Taylor, 1980).

128. *Cervical vertebrae* (ordered).—Short, length shorter than centra of anterior thoracics (0); long, length of centrum greater than or equal to the centra of the anterior thoracics (1); very long, length closer to twice the length of the anterior thoracics (2) (derived from Gingerich et al., 1995).

129. *Arterial canal for vertebral artery in cervical vertebrae 3–6.*—Posterior openings exterior to neural canal (0); inside neural canal (1) (Gentry and Hooker, 1988).

130. *Articulation between sacral vertebrae and illium of pelvis* (ordered).—Broad area of articulation between pelvis and S1 and possibly S2 (0); narrow articulation of pelvis with end of transverse process of S1 (1); articulation absent (2) (Geisler and Luo, 1998).

131. *Number of sacral vertebrae* (ordered).—One (0); two or three (1); four (2); five or six (3). Cannot be scored for taxa that lack articulation of vertebral column to ilium (Thewissen and Domning, 1992; Gingerich et al., 1995).

FORELIMB

132. *Scapular spine.*—Bears large acromion process that overhangs glenoid fossa (0); scapular spine with acromion process reduced or absent, does not encroach upon glenoid fossa (1); acromion process unreduced, directed anteriorly and does not encroach upon the glenoid fossa (2) (derived from O'Leary and Rose, 1995b; O'Leary and Geisler, 1999).

133. *Supraspinatus fossa of the scapula.*—Large, portion on neck faces laterally and is equal to or larger than the infraspinatus fossa (0); small, portion on neck faces anterolaterally and is smaller than the infraspinatus fossa (1).

134. *Entepicondyle of humerus.*—Wide, width 50% or greater than the width of the ulnar and radial articulation facets (0); narrow, 25% or less than the width of the ulnar and radial articulation facets (1) (derived from O'Leary and Rose, 1995b; Geisler and Luo, 1998).

135. *Entepicondylar foramen.*—Present (0); absent (1) (Thewissen and Domning, 1992).

136. *Distal articular surface of humerus.*—Restricted by medial edge of trochlea (0); expanded medially past trochlear edge to form convex surface (1) (Gentry and Hooker, 1988).

137. *Distal humerus intercondylar ridge be-*

tween capitulum and epicondyle.—Absent (0); present (1) (modified from Gentry and Hooker, 1988).

138. *Length of olecranon process.*—Short, <10% of total ulnar length (0); long, >20% of ulnar length (1) (derived from O'Leary and Rose, 1995b; O'Leary and Geisler, 1999).

139. *Posterior edge of ulna* (ordered).—Convex posteriorly (0); straight (1); concave posteriorly (2) (derived from O'Leary and Rose, 1995b).

140. *Radius and ulna* (ordered).—Completely separate (0); fused distally (1); fused completely (2) (Webb and Taylor, 1980).

141. *Proximal end of radius* (ordered).—Single fossa for edge of trochlea and capitulum of humerus (0); two fossae, for the medial edge of the trochlea and the capitulum (1); three fossae, same as state 1 but with additional fossa for the lateral lip of the humeral articulation surface (2) (Geisler and Luo, 1998).

142. *Distal articulation surface of radius.*—Single concave fossa (0); split into scaphoid and lunate fossae (1) (derived from O'Leary and Rose, 1995b; Geisler and Luo, 1998).

143. *Centrale.*—Present (0); absent (1) (Thewissen, 1994).

144. *Magnum and trapezoid.*—Separate (0); fused (1) (Webb and Taylor, 1980).

145. *Manus.*—Mesaxonic, axis of symmetry of foot passes along center of digit three (0); paraxonic, axis lies between digits three and four (1) (O'Leary and Geisler, 1999).

146. *Second metacarpal contact with magnum.*—Present (0); absent, excluded by proximal end of metacarpal three (1).

147. *Second digit of forelimb* (ordered).—Long, distal end of third phalanx terminates distal to distal end of second phalanx of third digit (0); reduced, distal end of third phalanx terminates proximal to distal end of second phalanx of third digit (1); highly reduced, metacarpal forms proximal splint or nodule (2); absent (3).

148. *Width of middle portion of second metacarpal* (ordered).—Wide, 130%> minimum width of second metacarpal >94% minimum width of third metacarpal (0); constricted, 78%> minimum width of second metacarpal >51% minimum width of third metacarpal (1); highly compressed, 36%> minimum width of second metacarpal >5% minimum width of third metacarpal (2).

149. *Fifth digit of forelimb* (ordered).—Long,

distal end of third phalanx terminates distal to distal end of second phalanx of third digit (0); reduced, distal end of third phalanx terminates proximal to distal end of second phalanx of third digit (1); highly reduced, metacarpal forms proximal splint or nodule (2); absent (3).

150. *Width of middle portion of fifth metacarpal* (ordered).—Wide, 100%> minimum width of fifth metacarpal >78% minimum width of third metacarpal (0); constricted, 70%> minimum width of fifth metacarpal >40% minimum width of third metacarpal (1); highly compressed, 35%> minimum width of fifth metacarpal >15% minimum width of third metacarpal (2).

HINDLIMB

151. *Greater trochanter of femur* (ordered).—Below level of head of femur (0); approximately same level as head of femur (1); elevated dorsally well beyond head of femur (2) (derived from O'Leary and Rose, 1995b).

152. *Third trochanter of femur* (ordered).—Present (0); highly reduced (1); absent (2) (Luckett and Hong, 1998; O'Leary and Geisler, 1999).

153. *Patellar articulation surface on femur.*—Wide (0); narrow (1) (O'Leary and Geisler, 1999).

154. *Tibia and fibula* (ordered).—Separate (0); fused proximally (1); fused proximally and distally (2) (Webb and Taylor, 1980).

155. *Fibula.*—Complete (0); incomplete (1) (Webb and Taylor, 1980).

156. *Proximal end of astragalus* (ordered).—Nearly flat to slightly concave (0); well grooved, but depth of trochlea <25% its width (1); deeply grooved, depth >30% its width (2) (derived from Schaeffer, 1947; O'Leary and Geisler, 1999).

157. *Astragalar canal.*—Present (0); absent (1) (Shoshani, 1986).

158. *Navicular facet of astragalus* (ordered).—Convex (0); saddle-shaped (1); V-shaped (2) (Schaeffer, 1947; Thewissen and Domning, 1992; Geisler and Luo, 1998).

159. *Distal end of astragalus contacts cuboid* (ordered).—Contact absent (0); contact present, articulating facet on astragalus forms a steep angle with the parasagittal plane (1); contact present and large, facet almost forms a right angle with the parasagittal plane (2).

160. *Long axes of proximal and distal articulating surfaces of astragalus.*—If extrap-

olated, form angle that is obtuse and opens medially (0); parallel, no angle formed (1) (modified from Gentry and Hooker, 1988).

161. *Proximal half of lateral surface of astragalus.*—Concave (0); flat (1) (modified from Gentry and Hooker, 1988).

162. *Lateral process of astragalus.*—Present, ectal facet of the astragalus faces in the plantar direction and its distal end points laterally (0); absent, ectal facet faces laterally and its long axis is parasagittal (1) (Schaeffer, 1947).

163. *Sustentacular facet of the astragalus.*—Narrow and medially positioned, lateral margin of sustentacular facet of the astragalus well medial to the lateral margin of the trochlea; (0) wide and laterally positioned, lateral margin in line with the lateral margin of the trochlea (1) (derived from Schaeffer, 1947; Geisler and Luo, 1998).

164. *Sustentacular facet* (ordered).—Completely separated from navicular/cuboid facet (0); medial edge of sustentacular facet continuous (1); completely continuous with cuboid/navicular facet (2).

165. *Articulation of calcaneus and cuboid.*—Flat, proximal articulating surface of the cuboid in one plane and corresponding surface of the calcaneus faces distally (0); sharply angled and curved, proximal surface of the cuboid has a distinct step between the facets for the calcaneus and astragalus (1).

166. *Cuboid and navicular.*—Unfused (0); fused (1) (Webb and Taylor, 1980).

167. *Cubonavicular and ectocuneiform.*—Separate (0); fused (1) (Webb and Taylor, 1980).

168. *Ectocuneiform and mesocuneiform.*—Separate (0); fused (1) (Webb and Taylor, 1980).

169. *Pes.*—Mesaxonic, axis of symmetry of foot passes along center of the third digit (0); paraxonic, axis lies between digits three and four (1); axis passes along center of digit four (2) (derived from Gingerich et al., 1990; Thewissen, 1994; O'Leary and Geisler, 1999).

170. *First metatarsal* (ordered).—Unreduced, length >50% length of third metatarsal (0); reduced, length <50% length of third metatarsal (1); highly reduced, metatarsal forms nodule or small splint or is absent (2) (O'Leary and Geisler, 1999).

171. *Second digit of hindlimb.*—Long, distal end of third phalanx terminates distal to

distal end of second phalanx of third digit (0); reduced, distal end of third phalanx terminates proximal to distal end of second phalanx of third digit (1); highly reduced, forms nodule or small splint (2); absent (3); reduced, distal end of phalanx terminates proximal to the distal end of the second phalanx of the third digit because the second metatarsal is 50% of the length of the third metatarsal (4).

172. *Width of the middle portion of the second metatarsal* (ordered).—Wide, 100%> minimum width of second metatarsal >75% minimum width of third metatarsal (0); constricted, 68%> minimum width of second metatarsal >27% minimum width of third metatarsal (1); highly compressed, 18%> minimum width of second metatarsal >9% minimum width of third metatarsal (2).

173. *Fifth digit of hindlimb* (ordered).—Long, distal end of third phalanx terminates distal to distal end of second phalanx of third digit (0); reduced, distal end of third phalanx terminates proximal to distal end of second phalanx of third digit (1); highly reduced, metatarsal forms nodule or small splint (2); absent (3).

174. *Width of middle portion of fifth metatarsal* (ordered).—Wide, 100%> minimum width of fifth metatarsal >70% minimum width of third metatarsal (0); constricted, 46%> minimum width of fifth metatarsal >36% minimum width of third metatarsal (1); highly compressed, 26%> minimum width of third metatarsal >10% minimum width of third metatarsal (2).

175. *Elongation of third metatarsal.*—Absent, 20%< length of third metatarsal <39% of the length of the femur (0); slight elongation, 47%< length of third metatarsal <54% of the length of the femur (1); substantial elongation, 63%< length of third metatarsal <95% of the length of the femur (2).

176. *Keels on distal ends of the metapodials.*—Present, restricted to distal and plantar surfaces (0); present and extended onto dorsal surface (or anterior surface in a digitigrade stance) (1) (Webb and Taylor, 1980).

177. *Fusion of third and fourth metatarsals.*—Absent (0); present (1) (Webb and Taylor, 1980).

178. *Anterior surface of distal ends of third and fourth metatarsals.*—Unfused (0); fused, fusion forms prominent gully between third and fourth metatarsals (1)

(Janis and Scott, 1987; Scott and Janis, 1993).

179. *Ventral edge of distal phalanges of foot.*—Distinctly concave (0); flat (1) (O'Leary and Geisler, 1999).

180. *Distal phalanges of foot in dorsal view.*— Phalanx compressed transversely (0); broad transversely, each phalanx is bilateral with central anteroposterior axis (1); broad transversely, each phalanx is asymmetrical (2) (O'Leary and Geisler, 1999).

INTEGUMENT

181. *Hair.*—Abundant to common on body (0); almost completely absent (1) (Gatesy, 1997; O'Leary and Geisler, 1999).

182. *Sebaceous glands.*—Present (0); absent (1) (Gatesy, 1997; O'Leary and Geisler, 1999).

STOMACH

183. *Right side of fornix ventriculi* (ordered).—Just lateral to dorsal mesogastrium (0); large, expanded anteriorly and laterally (1); hypertrophied, forms elongate blind sac (2); forms elongate blind sac, and sac divided into compartments by internal septa (3) (modified from Langer, 1974).

184. *Omasum.*—Absent (0); present (1) (Langer, 1974).

OTHER SOFT TISSUE

185. *Cavernous tissue of penis.*—Abundant (0); sparse (1) (derived from Slijper, 1936; Thewissen, 1994).

186. *Primary bronchi of lungs.*—Two (0); three, two on the right and one on the left (1) (Thewissen, 1994).

APPENDIX 3. CHARACTER CODINGS

The 176 morphological characters were coded for 68 taxa. The observations are based on specimens and references listed in appendix 1. N = character inapplicable; A=0+1; B=0+2; C=0+3; D=1+2; E=2+3; F=3+4; G=0+1+2; H=0+1+3; I=1+2+3. The matrix is available from http://herbaria.harvard.edu/treebase/ under study accession number S 589.

Taxon	10	20	30	40	50	60	70	80	90	100
Leptictidae	N000000001	0000000NNN	NN?NNON000	0011210001	000000A100	0000011110	0020000000	0100??2?01	0010000100	0000110020
Orycteropus	N0?0002N00	1000000NNN	NN?NNON?00	0000010001	0000001110	000000301?2	0021000100	0100220202	1??????01N	??????????
Rattus	1100000101	0011001001	10?3011002	?0010100D0	2000100100	0100000010	?230D10000	0000010101	0?3????01N	??????0?0
Vulpavus	?001000001	0001?1????	?????????00	0011C20001	0000101100	0?00110010	000010000?	0000021101	0019000100	0001A0?10
Canis	?1011N0001	0001001000	1200110101	00112200E2	0000101000	0000100010	0000201101	0100111001	0010000100	1000100010
Arctocyon	?0?0001000	000000????	?????????00	1030C20011	0001101121	0000001111	0012201110	000??21001	00?00?010?	0000000000
Hyopsodus	?0?00?0000	0101?0????	?????????01	1011?10012	0000101100	??00001111	0010120?00	0?00??1202	0000000100	0100011000
Phenacodus	?1?11N0010	??00?01???	?????0N000	A0D1C10032	0000101100	?00000D111	0010011010	0000020D01	0010000101	0100111000
Meniscotherium	?0?0??0010	0100?1????	?????????0?	?011C10001	0000102101	1?0100111A	0010001120	0001020212	0010000100	0000?110A0
Heptodon	N1?11N00?0	1101100NNN	NN?NNON?01	10?0C2??01	0010010?0?	??01102120	0010?20070	0000111110?	00100011N	0100111020
Hyracotherium	?1?11N0010	?101?1????	?????0N?0A	1021C20?12	0000101101	?0011011110	0001270?00	0000111102	0019000200	0100111010
Equus	01011N0A10	1100011101	0410010201	1001210002	0011112101	1100013112	002100A110	0000210212	001?20N10?	?10010?0?0
Mesohippus	?1011N0110	1101?11?00	0213110200	00D1210101	0001111110?	100001A11	1011D10000	0100121212	0010100200	01001A1020
Diacodexis pakist.	?0?0??0001	0??1??1000	A????1?A00	??11?10012	00?0101110	0100172711	?010270?0?	0101121101	0010020200	0000010?10
Wasatch Diacodexis	?000010021	0?01?1????	?????????0?	????210?01	0??2?0??17	??00?21??0	??2??2?210	A??0??1001	??1??2?0?0?	0000010210
Homacodon	?0??010001	?701?1????	?????????0?	0??22?10001	00101072?0	?00??12107	?710200?00	0??0??20??	0??2?202??	0002010210
Bunomeryx	??????0?7?	0??700100?	141C01?20A	?011BA0?03	0D?0000117	10001?1720	0000270700	0??2??1211	00?0?202??	0000011720
Gobiohyus	?0?11N0021	??01?1????	?????????0?	?021110002	0?0000?710	??01?02?11	0010201?00	0?00?1?01	??71000200?	0000011?20
Entelodontidae	1021IN2N11	1001011000	0200110200	202130NN34	0000001010	0000202113	0011200100	0010001002	0000000200	1001010110
Elomeryx	01011N1101	1101001000	0200110201	002130NN32	1010001010	?00110213	0021210110	0010112201	00??200200	1100011110
Hippopotamus	0101??2N??	110?011100	1003110201	1000320133	0000111010	1101D01033	0001D01100	0101100002	03300111N	10000?0110
Hexaprotodon	0?A???2N??	110?011100	10031?7201	1001320133	0000111070	1100101032	0001101100	0010111002	0030011100	0100011100
Sus	01011N2N11	0001011100	2200010202	200010NN34	?210111010	0000103103	1032010100	0000011202	03300112?N	1000101110
Tayassu	01011N2N11	100101110?	1210010201	20D030NN32	0001111110	1000103120	0011010100	0010001002	00110110?N	0100101100
Perchoerus	0101??1111	??7D00100?	120011010D	202030NN23	0010001110	0?0010311D	0021200100	0?10?21110?	00?10?1120B	1000111110
Agriochoerus	1000070001	0001011000	1200110202	001111002E	1210102110	1000101111	0010101110	0000011111	0020100B01	0000111120
Merycoidodon	1101N0001	0001011000	0100011?202	0021010013	1210101110	1000201102	1000200110	0000111111	0010100201	0100011120
Mixtotherium	?0?1?211??	????10100?	120011?200	10201A1104	1000002017	?00110071	0000200100	0?0??01012	0010000200	?100111?20
Cebochoerus	?1????2N11	??7?001?20	121?110201	0021HA1102	0000002072	?100111010	000?200?00	?00??A111?	00D?1?0D00	0000A0110
Cainotherium	1000??00??	0000001100	2410110101	1?2230NN02	0?00001100	1001202DA0	0110100100	0110311111	0010100200	00000A1120
Poebrotherium	11?11N0001	0001001000	2F00112101	1003310032	0100000110	?101212011	0121010110	0100121101	0010000200	1000001120
Lama	1?0??20001	0?0?0A1100	2400111202	1012310???	0000101110	000121111	0111070170	2A0A220D0?	0?10070?1N	A000021120
Camelus	11011N0001	0001011100	2400111101	1012220?0?	0000001110	110021211	0021000110	2100020?0?	C?1000?01N	0000001120
Xiphodon	??????00??	0?????1?0?	2?????1????	?1A2?D00??	??70??017?	??0??11??	0??A?00170	A00?A2?211	0000??0200	1000011??0

APPENDIX 3
Continued

Taxon	110	120	130	140	150	160	170	180	
Leptictidae	0020010001	0000010011	0100022120	2120000100	10221?2020	2210010020	0200000001	2022120000	??????
Orycteropus	?21?2?2???	?2?2?2?2??	?2?000100	3000000100	0000110010	1011010000	1000000001	0010010011	02????
Rattus	0020D?11??	1110?11??0	1100000100	1000100000	0000201010	2012011000	1122000000	0010000000	00A0??
Vulpavus	0022010000	0000000001	0100000???	?000000000	00?0200000	1A00000000	1011000010	0000010000	??????
Canis	0022211002	000000A00?	0100000100	1101100010	0010200000	0210021000	1000000012	1110A10000	000000
Arctocyon	0020001000	0000000000	0100022100	?020000000	0010200000	0000000010	1001000020	2?2?010001	??????
Hyopsodus	00100100A0	0000010000	0100002120	2020000000	0012??????	0000000000	2012?00000	A0A0?1?010	??????
Phenacodus	0101A1A20	0000010100	0100001102	2200000020	111210001A	2010010000	00A0000001	0011010011	??????
Meniscotherium	0010010120	0000010100	1100000100	2000000120	11010A1A1	2010000000	1000000001	A01010011	??????
Heptodon	000000000?	?110011000	1100021?0?	??01110020	11010A202	2010221210	1000000002	A113?10?11	??????
Hyracotherium	0010001000	0110011000	1100000100	3101101020	1112120112	2010021200	1000000002	A1??210011	??????
Equus	0010011120	0110010100	1101111100	3111110121	2110101313	2012122200	1001000002	1313220011	000000
Mesohippus	0010011020	0110011000	1101101100	3111101A20	2110100213	2010021210	1000000002	1213D10011	??????
Diacodexis pakist.	0010001000	1000000000	010100A100	1??2?07020	1?010?1?1	D110221220	21?2?00012	2?2?110000	??????
Wasatch Diacodexis	0010001000	1000000000	0101001100	1?01100??0	21??????G?G	1110221220	1110100112	?110210010	??????
Homacodon	0000000000	0000011000	010?1?2A2?	??????????	??????G?G	???A?11120	21?2??????	2G?G??????	??????
Bunomeryx	0010000010	0000010000	010?0?2???	????????2A	?1020A1A2	??2A221220	111?10???0	AAAA?00010	??????
Gobiohyus	0000000000	1000011000	010?2?????	??????????	??????????	??????????	??????????	?2?G??????	??????
Entelodontidae	0010001000	0000010000	0100000100	1111111022	2110211313	0210021320	1111100112	1313110010	??????
Elomeryx	0000010120	1000011000	0101000120	?101101120	211020??21	?210?22320	21?2100011	1111??0012	??????
Hippopotamus	00100N1012	1000010000	0B00001100	3101100122	1110201111	2210021220	1111100012	1110010012	1120??
Hexaprotodon	00100N1002	1000010000	0200000100	3101101122	2110201110	121?011320	1111100012	1010010012	1220??
Sus	00100N11A0	0000011000	0101001100	2111111120	2110211111	1210021320	0110100012	1111020012	000011
Tayassu	00100N1000	0000211000	0101001100	3111111122	2110211212	1?10021320	1110100012	2112021010	0000??
Perchoerus	0000001000	0000011A00	010A0?2???	??0???2??2	??????????	??????????	??????????	??????????	??????
Agriochoerus	0000010A22	1000000110	0101121110?	1100100020	21?0200001	0210021320	1110100112	0000010010	??????
Merycoidodon	0010010022	1000000100	0101021?00	2?01100020	21?0201110	0?10011320	1111100112	1111012010	0010??
Mixtotherium	0000010022	1000000000	010107????	??????????	??????????	??????????	??????????	??????????	??????
Cebochoerus	0010001001	1000010000	010107????	??????????	??????????	??????????	??????????	??????????	??????
Cainotherium	0010010122	0000010000	010107????	??????????	??????????	??????????	??????????	??????????	??????
Poebrotherium	0010011122	0000000000	0001101210	2111101022	2110211313	1212121321	0110100112	1313210010	??????
Lama	0010022122	?000000000	0101111210	3111100022	2110221313	1211121321	0111100112	13??211010	0010??
Camelus	0010001122	1000000000	0101101210	3121100022	2110221313	A21?221321	0110100112	1313211011	001011
Xiphodon	0000010020	1000000000	0101??????	???21?2020	2210201313	?21A?21E21	?1??100112	1313210010	??????

APPENDIX 3
Continued

Taxon	10	20	30	40	50	60	70	80	90	100
Eotylopus	?????????	?????1110?	231??1?D??	1111?D00?3	0?00???0??	??01D02??0	0020001??0	00??221201	0000000D00	0000011110
Leptoreodon	?????20??	??????????	??????????	??A1??????	0??0??11??	??0??02???	0??12????0	0????D1101	00110021N	?100011?20
Heteromeryx	?????????	??????????	??????????	A?D???????	?????A1??	??0??212???	??0??21??0	A????????	??????D??	??000011?D?
Protoceras	11011N0001	0001?1100?	0200111?201	10113100D3	0210101110	??01213011?	00?1111000	2000110101	1?11100200	?1000A1120
Odocoileus	10011N0101	1001011000	0113110201	01022200D3	0210100110	10202A2102	1101210000	0000220101	1?1?1000?N	01000A1120
Ovis	10011N0001	1001?11000	0213010201	01022100D3	0200100110	1011213112	1011200000	0000210111	1?1?10001N	0100001120
Bos	11011N0001	1?01001100	1403110202	A0012100E3	0200100110	0010213113	0011200000	1000220211	1012100110	0100001120
Tragulus	10001N0000	0001011100	2410111?101	0102310000	0?00000110	10002000A2	0011200010	0000110101	1?1110?01N	1000A?0100
Leptomeryx	10011N0011	0001011000	0110111202	0012210002	0210101110	1000201111	0100200?00	0000021211	0120100000	0100001120
Hypertragulus	?0011N0001	00?1?01???	1110011?201	0012010012	0210101112	?000001101	0100200?00	0000211111	??1?1100200	0000011?20
Amphimeryx	?0?0??00??	??????001??	2200111?202	00A031100?D	0??0100111?	??00?11121	000??200???	?00??D1D11	????????	000111?D0
Eoconodon	??00??00?20	20?1?1????	???????1??0?	1021C20022	0001001000?	??00000212?	?210101?10	0100012001	0??000100	0000000?00
Andrewsarchus	?????200??	??????????	???C???1?00	?02A?30?34	0001?1?D00?	??0011313??	00?120?110	0?0??1?01	00???00100	0?00?00?00
Hapalodectes hetang.	?000??0010	??00?0????	??????1??01	0101C10000	00011?1001	1100010010	00?0200101	000?01?001	00?0?0?100	0?001?0?20
Hapalodectes leptog.	??????????	??????????	???????1??00	???12220200	????101????	?????1E???	??????2??01	??????1?01	???2?00?0?	???2?0???0
Dissacus praenuntius	?0001ND??0	010???????	?????????A	???2220032	0001001????	??????????	?00?01?00?	?20??100?	????00?00	000120?20
Dissacus navajovious	?20??10??	012???????	??????????	?????????E	0001002???	??2?00111I	0?1?2???01	?20??100?	????00?00	000100?20
Mongolian Dissacus	?10011020	0?01?110??	?????1?00	0???D0022	0001002?01	?200?011?0	000?201?01	0??0?1?01	0010000100	0000100?20
Sinonyx	00??????20	0????1000	?100011?200	1030120023	0001?01?01	?000002101	0010211?00	0000010001	00???00100	0000A00?21
Pachyaena gigantea	????0???00	0????1100?	??01??2?A	0?E0?3003E	000100A???	??0002?10A	001A21??10	0000000001	?0?0?00D0?	1000100?21
Pachyaena ossifraga	??0???2??0	?1??????	???????20?	1?E2?E0?34	000100D00?	???A02111	0??0211110	A0??011001	00?0000100	1000100?22
Mesonyx	?00001??00	1101?11000	0??0?1?200	1031120034	0001000001	??0002?21?	0010??1110	000???1011	000000010?	A000100021
Synoplotherium	????????00	?20??1??00	0202??1?200	1031?20034	0001001001	??00002111	0010111110	000?001001	?0?00?0?0?	??0??20?21
Harpagolestes	0???????00	???0?1000	01?011?200	1030120034	0001101000?	??00102111	00111111A	00??000001	?0?00?011N	1?00100??2?
Pakicetus	?A?11N1111	01?2001010	1001110100	0031221133	0000001?11	??2?0???????	???????0?	??0000?001	??????02A?	?01101000?
Ambulocetus	?????????	?11???1011	2101?1?00D	10???????	???????10	??00??3???	0???00???1	?00101000?	?0?0?00D0?	??11?0?0?
Remingtonocetus	?1?11N1?1	?112?11?11	?11111012	0031??1?1	0000021010	??00??3??3	0032201201	0??????2?2	?1???????	??1???????
Georgiacetus	11?11N1111	??12011011	2111111012	0030230123	0000021010	??0100??1E	00A1201?01	1001000011	010??0200	021111??A?
Protocetus	11?11N11??	??12011011	2111110012	0070220113	0000002?01?	?00100??1?	00?1?01?01	1????0????	??0??01??	021107??1?
Basilosaurus	?1?11N1111	12131110??	2??2????12	0020230122	0000021012	??01100?1?	???1201?11	D?010?1011	0100100201	1011000??1
Balaenoptera	0111N2N11	1213111011	2003011011	1001230114	0000022110	210101??31	00??00?20?	2000100001	?????2N???	?????N????
Tursiops	0111N2N11	1213111011	2113011012	11020101?D	0000??1010	00?10??230	20?1??0??1	2001?0??1	?????N???	?????????
Delphinapterus	0111N2N11	1113111010	1113011011	01N1011131	0000100010	0101007030	2001000011	20?1??0?11	?0?0??????	?????????
Physeter	0111N2N11	1?13111010	2113011012	10NN210124	00001B??10	0101007030	2001000001	2001000001	12N?NN??NN	NNNNN?NNNN

APPENDIX 3
Continued

Taxon	110	120	130	140	150	160	170	180	
Eotylopus	0000001120	1000000000	00011A????	??11100?22	111021A2A2	??1??21222?	0110100?12	1313110010	0?????
Leptoreodon	0000010022	1000000000	0102??????	?????00???	??????????	121??1????	??????0???	??????????	??????
Heteromeryx	0?1??2102D	000???????	??????????	EP1110002B	21102??D1D	??1??21E20	01??100???	?????10010	?????
Protoceras	0010001122	A000000000	0101101?00	E111101020	21?0201111	2?11021320	0110100111	1313110010	?????
Odocoileus	0010001122	1000000000	0201111?00	2111101121	21?12?1313	22111D1221	0112110112	1313221110	??31??
Ovis	0010011122	1000000000	0101?11100	2111111021	2111121313	1211121321	0112110112	1313221012	003111
Bos	0010011122	1000000100	0101111100	311111112D	21112N1313	2211121221	0111110112	1313211110	003111
Tragulus	0010010122	1000000100	0101101100	21?110102A	2111201212	D212121321	0111110112	111221111B	0031??
Leptomeryx	0010001122	1000000000	0D01101100	3?11101020	2211201212	2211121321	0111110112	1312211010	??????
Hypertragulus	00A0001112	1000010000	0200001???	?101101022	21?020?2?2	1?12021321	?111110110	1212110010	??????
Amphimeryx	0000010120	1000010000	0101???????	??????0??A	??????????	???????????	??????????	??????????	??????
Eoconodon	0020011001	0000000000	0?0?0?????	??00000??A	??????????	????10????	100???????	??????????	??????
Andrewsarchus	0?0?001000	1000?10000	?A000?????	??????????	??????????	??????????	??????????	??????????	??????
Hapalodectes hetang.	10?1201102	1000100001	0010??????	??????????	??????????	??????????	??????????	??????????	??????
Hapalodectes leptog.	1020201102	1000100001	0010??????	??????????	??????????	??????????	??????????	??????????	??????
Dissacus praenuntius	1020?2?022	2000100001	021?0?????	?????0????	??????????	??????????	??????????	??????????	??????
Dissacus navajovious	1020200002	2000100001	0D10000?00	??00000?D0	2?????????	?21??10110	1000000???	?0?0?100??	??????
Mongolian *Dissacus*	1020200002	2000100001	0210000??0	??00000?20	2?0020A0A0	1010010110	1000000?72	?0?0?100??	??????
Sinonyx	?021200002	2001100001	0210??????	??????????	??????????	??????????	??????????	??????????	??????
Pachyaena gigantea	1121200002	1000100001	0210000??0	?0?1000120	2100200010	???0?10210	?0????????	?????????11	??????
Pachyaena ossifraga	1222200002	1000100001	0210000100	1?01000120	210020A0A0	2010?10210	1000000012	A0?0010011	??????
Mesonyx	1137201102	2000100001	0210001??0	1101000120	21002012?0	1010011210	0010?10011	0010?10011	??????
Synoplotherium	1?22?211??	D000102??1	0212?0?1??	1001000120	2100200000	1010071212	?00?000012	1010010011	??????
Harpagolestes	213?201102	2000100001	0210?????	??71000120	2?????????	?0????????	??0???????	?????1????	??????
Pakicetus	2?10201002	2001007??1	0011?0????	??????????	??????????	?0????????	??????????	??????????	??????
Ambulocetus	?111201110?	2001?00???	001007?00	2?????120	0100?0?070	101B?10?7?	????????1?	A0A0110011	??????
Remingtonocetus	??0??01?02	2007?0000?	0?10000100	2?????????	??????????	2?0???????	??????????	??????????	??????
Georgiacetus	1?11201002	2001?00001	0010??002	0?????????	??????????	??????????	??????????	??????????	??????
Protocetus	1?1??01102	2007??0???	0??00000??	??????????	??????????	??????????	??????????	??????????	??????
Basilosaurus	2131221002	2000?0000?	0?00000002	0211100120	??01?2?2??	2??20?????	????2A?222	E?A?000?0??	??????
Balaenoptera	????NN?N?	N00???????	??00??0N	??????????	NNNN??????	NNNN??????	?????????N	NNNNNONN??	110011
Tursiops	??????????	0?70000001	0211107020	0211107020	0??201A1A	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	110011
Delphinapterus	??????????	??70000000	??70000000N	0211100020	01??100010	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	1100??
Physeter	NNNNN?N?N	?NNNNNNNN	NNN0ON0OON	0211100020	0??0?0010	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	1100??